Specialization, evolution and coexistence in a community context

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Ellen van Velzen

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Chapter 1

General introduction

Ellen van Velzen

Ecology and evolution have traditionally been separate fields of study, despite the obvious ways in which ecological and evolutionary dynamics are intertwined. An important reason for this separation has been the view that ecological and evolutionary processes occur on vastly different time-scales, an idea that goes back all the way to Darwin: "We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages." (Darwin 1859). Almost a century later, in his book *Growth and Regulation of Animal Populations*, Slobodkin (1961) referred to the two timescales as "ecological time" and "evolutionary time"; ecological time corresponds to a short period of about 10 generations, while evolutionary time refers to timespans on the order of half a million years. Because evolution was long considered to be too slow to impact ecological dynamics in any meaningful way, any possible interactions between the two processes were neglected until recently. However, rapid evolutionary change has been found to occur since the 1980s (Endler 1986), and has continued to mount ever since (see e.g. Thompson 1998; Carroll et al. 2007; Hendry et al. 2007). As a consequence, interest in the ways that ecological and evolutionary processes affect each other has grown; this has been referred to as "The newest synthesis" (Schoener 2011).

Ecology and Evolution

That ecology matters for evolution is immediately intuitively obvious, as it is the ecological environment – biotic factors such as temperature or nutrient availability, but also the presence and abundance of conspecific or heterospecific competitors, predators, prey, parasites or mutualists – to which a species is adapting. A classic example of this is character displacement: divergent trait evolution driven by the presence of competitors to reduce resource competition (Lack 1947; Brown and Wilson 1956; Schluter et al. 1985; Schluter and McPhail 1992). For example, the introduction of the larger competitor *Geospiza magnirostris* triggered evolution of smaller beak size in the native *G. fortis* on the Galápagos island Daphne Major; *G. magnirostris* was a superior competitor for larger seeds on the island, driving *G. fortis* to specialize on smaller seeds (Grant and Grant 2006). This type of competition-driven evolution has been thought to be a driving force in speciation and adaptive radiations, ultimately being a strong driving force of diversity (Schluter 1994; Schluter 2000; Rundle and Nosil 2005; Pfennig and Pfennig 2010).

Aside from competition, interactions between trophic levels are a major driving force in evolution, including the evolutionary origins of diversification. Plants suffering damage from herbivory have evolved a vast array of defensive strategies, sometimes at great cost to their growth or reproduction (6-45% in controlled background studies, and 8.7-73% in studies of natural populations, Strauss et al. 2002); moreover, there is evidence that an escalating arms race between plant defenses and herbivore adaptations has caused the huge diversity in plants and insect herbivores (Becerra et al. 2009; Futuyma and Agrawal 2009). As a last example of ecological interactions as a driving force for evolutionary diversification, predation has been implicated in adaptive radiations: for example, radiations in camouflage in stick insects (Nosil and Crespi 2006), morphological defenses in dragonflies (Petrin et al. 2010) and armour in sticklebacks (Marchinko 2009).

Overall, speciation as a result of divergent selection imposed by the ecological environment is extremely well-supported (Dieckmann and Doebeli 1999; Schluter 2001; Rundle and Nosil 2005); it is abundantly evident that ecological interactions have played an important role in driving the origins of diversity.

Evolution and ecology

While ecology obviously affects evolution, the converse – that evolutionary change affects evolution – is true as well. Natural selection and population dynamics are closely linked, as both are determined by the births and deaths of individuals (Coulson et al. 2006; Hanski and Saccheri 2006; Pelletier et al. 2007; Coulson et al. 2010); assessing fitness is ultimately counting offspring transmitting genes to future generations, so population dynamics can be affected by natural selection (Kokko and Lopez-Sepulcre 2007; Schoener 2011). Adaptive evolution after an environmental change can magnify, offset or even reverse the population decrease caused by the change (Abrams 2014). Indeed, the concept of evolutionary rescue depends critically on this interplay: a population that has become maladapted due to sudden environmental change can be "rescued" from extinction by rapid evolutionary adaptation to the new environment (Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007; Bell and Gonzalez 2009).

When selection acts on a trait involved in ecological interactions with other species, like competition or resistance against herbivory, the ecological effects can be even more dramatic, and examples of evolution affecting ecological dynamics abound. Genetic variation within plant species affects the composition of arthropod and pathogen communities found on individual plants (Barbour et al. 2009; Busby et al. 2013); evolutionary change in life-history traits in a plant population can cause changes in arthropod abundance and diversity (Johnson et al. 2009). Ecological consequences can also reach farther than just one trophic level: for example, in the tropical tree genus *Inga*, which has >300 species and has radiated recently, neighbouring trees differ more strongly in antiherbivore defenses than random, suggesting divergent evolution in various types of defenses against herbivores allows coexistence of many *Inga* species closely together (Kursar et al. 2009). In another study, the experimental manipulation of adaptation (reducing camouflage in stick insects) not only reduces abundance of stick insects, but through an increase in bird predation, reduces the abundance and species richness of the co-occurring arthropod community, ultimately decreasing herbivory on host plants (Hendry et al. 2007; Farkas et al. 2013). Such trophic cascades may be expected in other systems where predation is affected by evolution. Another recent example is the effect of phenotypic differentiation between landlocked (freshwater) and anadromous (migrating between freshwater and marine habitats) alewives: differences between the two types in morphology and foraging behaviour strongly affect the zooplankton community, cascading down to phytoplankton abundance and composition (Post et al. 2008).

Effects of evolution can reach even further than direct species interactions: ecosystem functioning itself can be impacted. Theoretical study has shown that evolution of plant defense against herbivory and co-evolution of plants and herbivores can both impact nutrient dynamics, and through this the total productivity of the system (Loeuille et al. 2002; Loeuille

and Loreau 2004). Ecosystem effects have been demonstrated in empirical systems as well: the effect of prey evolution in response to high or low predation in Trinidadian streams causes divergence in ecosystem functioning, affecting primary production, leaf decomposition rates and nutrient flux (Palkovacs et al. 2009; Bassar et al. 2010). Speciation through adaptive radiation in sticklebacks has been shown to change the ecosystem from one dominated by phytoplankton and small zooplankton to one dominated by small zooplankton and small invertebrates (Harmon et al. 2009; Seehausen 2009), in turn affecting the composition of dissolved material and through this the intensity and colour of light under water. As light influences vision and mating preference, changes in light penetration brought about by speciation may affect whether further speciation is possible (Seehausen et al. 2008; Seehausen 2009). This is a prime example of an eco-evolutionary feedback loop, where evolutionary and ecological dynamics mutually affect each other. Eco-evolutionary dynamics and feedbacks will be the focus of this thesis.

The interplay of ecology and evolution: eco-evolutionary dynamics

At the basis of eco-evolutionary dynamics is the idea that ecological and evolutionary processes can interact, creating novel outcomes that would not be found if either were neglected. As a growing body of evidence suggests rapid evolution is possible, and perhaps even common (Thompson 1998; Reznick and Ghalambor 2001; Hairston et al. 2005; Hanski and Saccheri 2006; Carroll et al. 2007; Ellner et al. 2011), interest in eco-evolutionary dynamics has skyrocketed (Pelletier et al. 2009; Post and Palkovacs 2009; Schoener 2011; Strauss 2014). However, evolution does not need to be very rapid to cause eco-evolutionary feedbacks. While still assuming evolution and ecology operate on different time-scales, adaptive dynamics is one tool that has been developed to account for one specific type of eco-evolutionary interaction, frequency-dependent selection (see Box 1).

In a classic experiment, Yoshida et al. (2003) demonstrated the effect of evolution on predator-prey dynamics in an algal-rotifer system: algae facing a trade-off between growth and grazing resistance underwent rapid evolution depending on predator abundance, with fast-growing (but vulnerable) genotypes being selected for under low grazing pressure, while high predation pressure resulted in selection for grazing-resistant (but slow-growing) genotypes. The relative frequencies of the vulnerable and resistant genotypes in turn affected predator densities; the resulting predator-prey cycles were different from any single predator-single prey model without evolution (Shertzer et al. 2002). This result – that evolution of defense in prey can dramatically alter predator-prey dynamics – has been confirmed by other experimental studies (Meyer et al. 2006; Duffy and Sivars-Becker 2007; Yoshida et al. 2007; Turcotte et al. 2011) as well as theoretical work. Models have shown that prey evolution as well as predator-prey coevolution can either generate population cycles in systems that would otherwise be stable, or stabilize systems that would otherwise exhibit cycles (Abrams and Matsuda 1997a; Abrams and Matsuda 1997b; Abrams 2000). Prey evolution or predator-prey adaptation (either through rapid evolution or phenotypic plasticity) can generate anti-phase and cryptic cycles (Jones and Ellner 2007; Mougi and Iwasa 2011; Mougi 2012), and the effect of prey evolution

on two-predator food webs can result in chaotic predator-prey dynamics (Ellner and Becks 2011).

The ability of evolution to change, stabilize or destabilize predator-prey cycles is one example of how eco-evolutionary dynamics shape trophic interactions. This can further affect ecological or evolutionary dynamics: for example, Yamamichi et al. (2011), in a theoretical study on competition between defended, undefended and a phenotypically plastic prey, found that phenotypic plasticity stabilized predator-prey dynamics; in turn, this caused phenotypic plasticity to lose its selective advantage over the fixed phenotypes of the specialists, resulting in complex eco-evolutionary dynamics. A similar effect is seen in a model of generalist-specialist coexistence with generalist switching: the stabilization provided by the switching generalist allows specialists to invade, contributing to specialist-generalist coexistence (Abrams 2006).

Eco-evolutionary dynamics can also affect population abundances in predator-prey (Abrams 2012; Abrams 2014), herbivore-plant (Loeuille et al. 2002; Loeuille and Loreau 2004) and plant-mutualist-exploiter interactions (Jones et al. 2009), and through this affect species extinction or coexistence (Lankau 2011; Northfield and Ives 2013).

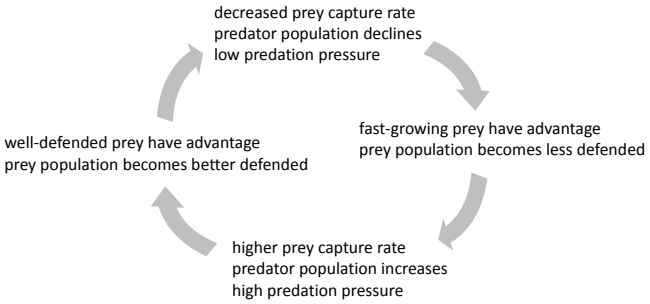

Figure 1.1 Eco-evolutionary feedback loop in the algae-rotifer system described in Yoshida et al. (2003).

Evolution of stability: eco-evolutionary dynamics and coexistence

A major focus of this thesis is on the coexistence of species competing for the same resources. While the ecological mechanisms allowing coexistence have a long history of theoretical study, the effects of combining these mechanisms with evolutionary dynamics have only come into consideration recently as interest in eco-evolutionary dynamics has grown (see e.g. Lankau 2011). The effect of adding evolution to well-established ecological models for coexistence, it turns out, is far from straightforward.

Abrams (2006b), looking at generalist-specialist coexistence on two resources, found that coexistence was more likely when the generalist could adapt to whichever resource was at higher abundance. This result directly contradicted a previous model that found that specialist-generalist coexistence was less likely when evolution was allowed than in a purely ecological model (Egas et al. 2004). Adding more confusion, a later study (Abrams 2006a) found that the speed of evolution relative to ecological dynamics played a role, and rapid evolution caused coexistence to collapse. Similar contradictory results have been found when evolutionary

dynamics were included in a variety of ecological scenarios. Studying the coexistence of two species facing a growth-competition trade-off on a single fluctuating resource, Kremer & Klausmeier (2013) found that evolution widened the range where coexistence was possible; but coexistence was facilitated most by slow evolution, while rapid evolution collapsed coexistence completely, as it did in the case of specialist-generalist coexistence on fluctuating resources (Abrams 2006a). In contrast, a model studying coexistence through niche divergence or niche convergence found that the speed of evolution positively impacted coexistence, with most extinctions occurring when evolution was slow (terHorst et al. 2010). These contrasting effects are the result of the different roles evolution plays in coexistence. In all scenarios, coexistence is enabled by niche divergence in resource consumption; but while faster evolution leads to faster divergence when resources are static, in fluctuating environments fast evolution allows the consumers to track the environment, collapsing coexistence because this strategy outcompetes all others.

Evolution has been found to either promote or impair coexistence in other scenarios. It can promote coexistence of competitors for nutritionally complementary resources (Vasseur and Fox 2011), or through neighbour-dependent selection, allowing coexistence under conditions where ecological processes alone would have led to competitive exclusion (Vasseur et al. 2011). On the other hand, Shoresh et al (2008) found that evolution exacerbates the paradox of the plankton, dramatically reducing the number of species that are able to coexist on a limited number of resources. Other cases in which evolution destroyed stable ecological coexistence include the evolution of handling time (Kisdi and Liu 2006) or of life-history traits not directly related to competition (Mougi and Nishimura 2006; Mougi and Nishimura 2007). In general, how adding evolution to ecological models – or, conversely, adding ecological dynamics to evolutionary models (see e.g. Loeuille and Leibold 2008; Zhang and Hui 2011) – affects coexistence appears to strongly depend on assumptions about the ecological scenarios under study, and the outcome of eco-evolutionary dynamics is not necessarily easy to predict.

This thesis

In this thesis I develop theoretical models to study eco-evolutionary dynamics in the context of trophic interactions; chapters 2 and 3 focus on plant-herbivore interactions, and chapters 4 and 5 on host-parasitoid interactions. Using the tools of adaptive dynamics and simulations (individual-based or similar), my focus is on conditions that allow for evolutionary branching, coexistence of different strategies, or both.

In **chapter 2** I study the effect of including competition between plants on herbivore evolution. Based on a well-established model for the evolution of generalist and specialist herbivores on two plant species, this model can generate more complicated eco-evolutionary dynamics as herbivore evolution affects the interactions between the two plant species, as well as between plants and herbivores. Using simulations to allow for evolutionary branching and extinction of herbivore strategies, I attempt to identify which types of herbivores can evolve and coexist under different conditions (trade-off strength and plant growth rate).

In **chapter 3** I study the evolution of plant defense against herbivory, comparing two different types of cost for the plant: direct cost (lower growth rate) and an ecological cost (lower competitiveness), a type of cost that is common in nature but has never been studied theoretically before. Additionally, I compare the effects of generalist and specialist herbivores on plant defense: feedback between plant evolution and herbivore abundance is present only in the latter case, making a direct comparison between the absence and presence of an eco-evolutionary feedback possible.

In chapters 4 and 5 I use a multiparasitoid-host system to study the conditions allowing coexistence of two parasitoid species; these models were inspired by the puzzling coexistence of *Nasonia vitripennis* and *N. giraulti* in Eastern North America. In **chapter 4** I focus solely on coexistence, studying the effect of distribution overlap, level of within-host competition between larvae, and asymmetric within-host competition.

In **chapter 5** I develop an evolutionary simulation based on the same host-parasitoid model. Inspired by the empirical observation that *N. giraulti* prefers multiparasitizing over parasitizing an empty host, I simulate the evolution of host preference (expressed as the clutch sizes when parasitizing unparasitized and parasitized hosts), where superparasitizing carries the advantage of allowing the female to economize on the production of venom required to kill the host (venom production is assumed to be costly and to trade off with fecundity). In this chapter, my focus is on the conditions allowing for evolutionary branching into different host use strategies.

In **chapter 6** I briefly synthesize the results of this thesis, and show some preliminary results indicating interesting future directions.

Box 1: Adaptive Dynamics

One way in which ecology and evolution affect each other is through frequency-dependent selection, where the fitness of an individual is determined not just by its own strategy (e.g. the amount of resources allocated to defense against predators), but by the strategy of other individuals in the same population as well (Heino et al. 1998). Adaptive dynamics is an extension of evolutionary game theory developed to determine the course of evolution in traits subject to frequency-dependent selection. It explicitly recognizes the interplay between ecological and evolutionary dynamics: the ecological state of the system is shaped by individuals' traits, and in turn determines the selective forces acting on those traits. The fitness of an invading mutant (and thereby its ability to successfully invade the population) depends on the trait values of the current ("resident") population, and the fitness landscape changes as the trait evolves through repeated invasion and establishment of mutants.

Potential endpoints of evolution are found at the trait values for which the local selection gradient disappears; these points are known as *evolutionarily singular strategies*. Whether evolution progresses towards or away from these singular strategies, and what happens after a singular strategy is reached, is determined by two properties: *evolutionary stability* and *convergence stability*. Convergence stability determines whether a singular strategy is attracting or repelling, meaning a population starting at different trait values will evolve towards or away from the singular strategy, respectively. Evolutionary stability determines whether the singular strategy is a fitness maximum or a fitness minimum for the population. If it is a fitness maximum, there are no mutant strategies close to the singular strategies that have a higher fitness than the resident; the resident strategy is immune to evolutionary invasion, and is said to be evolutionarily stable. If it is a fitness minimum, however, mutants on either side of the resident strategy can invade; the strategy is evolutionarily unstable.

Of particular interest are those singular strategies that are both *convergence stable* and *evolutionarily unstable*: this combination of stability properties can lead to evolutionary branching (Geritz et al. 1997; Geritz et al. 1998; Geritz et al. 1999; this thesis, chapters 2, 3 and 5).

Chapter 2

The evolution and coexistence of generalist and specialist herbivores under between-plant competition

Ellen van Velzen, Rampal S. Etienne

ABSTRACT

Consumer-resource models have been used extensively to study the evolution and coexistence of generalist and specialist consumers. However, current consumer-resource models do not take into account competition between resources or only incorporate intraspecific competition phenomenologically with, for example, a logistic growth function. Here we mechanistically incorporate competition in an existing two-resource model, by introducing nutrient-limited resource growth and setting the total amount of nutrients (free, or contained in consumers and resources) to a fixed value. In addition to the three combinations of generalists and specialists found in previous models, we find four other evolutionary outcomes, depending on the strength of the consumer trade-off: coexistence of one specialist and a generalist, and three types of evolutionary cycling. Furthermore, which outcomes are most likely depends strongly on the combination of intrinsic growth rate of resources and the total amount of nutrients in the system. Our results suggest that the realistic assumption of nutrient competition may shed new light on the evolution of the multitude of strategies in real systems.

INTRODUCTION

Studying the evolution of a consumer facing a trade-off in consuming two resources has a long tradition (Levins 1963; Lawlor and Maynard Smith 1976; Abrams 1986; Wilson and Yoshimura 1994; Egas et al. 2004; Abrams 2006a; Abrams 2006c; Rueffler et al. 2006; Rueffler et al. 2007). Theory on systems without oscillations suggests that the outcome of evolution depends on the shape of the trade-off: a weak trade-off should lead to the evolution of a generalist, whereas a strong trade-off should give rise to two specialists (Abrams 1986; Egas et al. 2004; Rueffler et al. 2006; Rueffler et al. 2007).

Although according to the principle of competitive exclusion, no more than n species can coexist on n resources, this is well known to be false for nonequilibrium systems (Armstrong and McGehee 1976; Levins 1979; Armstrong and McGehee 1980; Huisman and Weissing 1999). Wilson & Yoshimura (1994) showed that, in a two-habitat model for specialization, fluctuations in resource abundance can lead to a trimorphic state with two specialists and a generalist. However, their model does not include evolutionary change in the herbivores. Egas et al. (2004) included evolution, and concluded that the evolution of all three types was possible, but under very restricted scenarios.

Their model does not include plant dynamics, however. For a full picture of the possible outcomes, both consumer and resource dynamics should be considered. Abrams (2006c) used a consumer-resource model with explicit dynamics for both consumers and resources. Contrary to the findings of Egas et al. (2004) this model does result in the coexistence of all three types, driven by fluctuations in resource abundance. These results were confirmed with an evolutionary model (Abrams 2006a), which found gradual evolution leading to the coexistence of a generalist with two specialists, both for endogenous and exogenous sources of variation. Evolution gives rise to one generalist when the trade-off for herbivores is weak; to two specialists when it is strong; and to all three when it is intermediate.

Even this study still has some limitations. Most importantly, like all others, it assumes that the two resources do not interact (apart from apparent competition if they share consumers): there is no direct competition or facilitation between the two resources. However, when we interpret the consumers and resources as e.g. herbivores and plants, respectively, there are a large number of potential interactions. Plants may compete over space, over light, over water or plants; conversely, they may facilitate one another, e.g. by preventing evaporation or shielding from herbivores. All of these may impact plant dynamics, and by that the course of evolution in herbivores.

In this study, we modified the model used by Abrams (2006a) to consider the evolution of herbivores on two plant species competing over nutrients, a well-established factor limiting plant growth (Howarth 1988; Vitousek and Howarth 1991; Elser et al. 2007). Competition between plants should lead to antiphase oscillations in plant abundance (Vandermeer 2004). These oscillations may lead to the evolution of trimorphism in herbivores, as is the case in Abrams (2006a); but it may also cause different evolutionary dynamics altogether.

To study this, we used a combination of two methods. Because the inclusion of competition makes the system no longer analytically tractable, we used numerical procedures to study the course of evolution. First, we used simulations to track the evolutionary change in herbivore preference through time. Second, we used pairwise invasibility plots (PIPs) to look for the existence and position of evolutionarily stable strategies and branching points, to confirm the results of the simulations.

METHODS

Model setup

We used a simulation model with two plants, adapted from Abrams (2006a; 2006c). We incorporated competition into the model by assuming a fixed and finite nutrient pool. Nutrients are utilized by plants, whose growth rate is limited by the amount of nutrients available. Because they use the same nutrients, this leads to indirect competition between plants. Nutrients are recycled into the system and become available again to plants through plant and animal death, and through consumption of plant material not digested by the herbivores, making the system an entirely closed loop.

The plants were completely equivalent in all our simulations: their growth rate, dependence on the available nutrients, and their nutritional value to the herbivores are equal. They only differ in a trait that affects the preference of the herbivores, but does not directly affect their vital rates.

Ecological dynamics

The ecological dynamics of the system are determined by a system of differential equations, adapted from Abrams (2006a; 2006c). Plant and herbivore dynamics are described by the following equations:

$$\frac{dP_i}{dt} = \left(r \frac{F(t)}{F(t)+T} \frac{1}{c_p} - d_P \right) P_i(t) - \sum_{j=1}^{N_H} C_{ij}(P_i, H_j, x_{ij}) \tag{2.1}$$

$$\frac{dH_j}{dt} = e \frac{c_P}{c_H} \sum_{i=1}^{N_i} C_{ij}(P_i, H_j, x_{ij}) - d_H H_j(t) \tag{2.2}$$

Here P_i and H_i are plant and herbivore biomass, respectively, and F is the amount of (free) nutrients available to plants. r is the intrinsic growth rate; T is the total amount of nutrients in

the system; d_P and d_H are the per capita death rates for plants and animals, respectively; c_P and c_H denote the conversion factors between nutrients and plant or animal biomass; e is the conversion efficiency (the proportion of nutrients in the consumed material that is converted into herbivore biomass); C_{ij} denotes the consumption of plant i by herbivore j, and is given by

$$C_{ij}(P_i, H_j, x_{ij}) = \frac{aP_i(t){x_{ij}}^n}{1 + t_h a\left(\sum_{i=1}^{N_P} P_i(t){x_{ij}}^n\right)} H_j(t), \tag{2.3}$$

a Holling type II functional response (Holling 1959), using the same trade-off structure as Abrams (2006a); x_{ij} is the preference, or the proportion of the total time herbivore j spends feeding on plant i, where the two values must sum up to 1. This assumes a direct trade-off in the rate of attack on the two plant species: time spent feeding on one plant species cannot be spent on feeding on the other. A herbivore with $x = 1$ is completely specialized on plant 1, whereas $x = 0$ means complete specialization on plant 2. In this trade-off, n is the coefficient that determines the shape of the trade-off; $n < 1$ gives a concave trade-off where generalists have the highest fitness, whereas $n > 1$ gives a convex trade-off, where the more extreme phenotypes have an advantage and specialization is favored. $n > 1$ is required for any other evolutionary outcome than only generalists; this appears to be a reasonable assumption (O'Hara Hines et al. 2004).

The dynamics of the pool of available nutrients are given by the following equation:

$$\frac{dF}{dt} = c_P \sum_{i=1}^{N_P} d_P P_i(t) + c_H \sum_{j=1}^{N_H} d_H H_j(t) + (1-e) c_P \sum_{i=1}^{N_P} \sum_{j=1}^{N_H} C_{ij} - \sum_{i=1}^{N_P} r \frac{F(t)}{F(t)+T} P_i(t) \tag{2.4}$$

The nutrient pool is replenished by death of plants and herbivores (first and second term) and consumed plant biomass that is not converted into herbivore biomass (third term), and it is depleted when plants take up nutrients for growth (fourth term).

Setup of the simulation and evolutionary dynamics

Given the complexity of all the interactions, the above model is not analytically tractable. We therefore used simulations to study the result of this interplay between ecological dynamics and evolution. Herbivores are represented in the simulation as a large number of lineages (typically 400), each interacting with the two plant species. Each lineage has a value for x_{ij} between 0 and 1; at the start of the simulation, their initial values are drawn from a normal distribution with a standard deviation of 0.1. In each timestep, the ecological dynamics of plants, herbivores and available nutrients are determined by the above equations.

Table 2.1 List of parameters used in the model.

Parameter	Description	Value
r	Plant intrinsic growth rate	0.5 – 2
T	Total nutrients in the system	$2.5 \cdot 10^6$ – $6.5 \cdot 10^6$
n	Trade-off strength (higher = stronger trade-off)	1.1-3.6
a	Herbivore attack rate	$1 \cdot 10^{-5}$
t_h	Handling time	0.1
e	Conversion efficiency	0.25
c_P	Conversion factor between nutrients and plant biomass	1.0
c_H	Conversion factor between nutrients and herbivore biomass	2.0
d_P	Death rate of plants	0.05
d_H	Death rate of herbivores	0.4

Evolution is simulated by allowing the lineages to "mutate": each timestep, each lineage has a small mutation probability. A mutation splits a lineage into two, spawning a daughter lineage and dividing its biomass between them. The preference value for the daughter lineage is drawn from a normal distribution around the parent value, with a small standard deviation (typically 0.01). The daughter lineage then takes the place of the lineage with the lowest biomass which goes extinct. The total number of lineages is thus constant throughout the simulation.

Simulations were run for 100,000 timesteps, after which the end result (what coalition of herbivores evolved) was recorded. We explored a range of values for three parameters very likely to affect the outcome of evolution: n, the trade-off coefficient; and r and T, plant intrinsic growth rate and total nutrients, because these will strongly affect plant abundances.

A total of eight different outcomes was found (including extinction of the herbivores) for a range of n, r and T values: r ranged from 0.5 - 2; T ranged from, $2.5 \cdot 10^6$ to $6.5 \cdot 10^6$; and n ranged from 1.1 to 1.8 (a subset was run over a wider range, 1.0 - 3.6, to test whether the patterns also hold beyond this range).

Pairwise invasibility plots

To check the results of the simulations, specifically what happens after the herbivores reach the stage of generalist-specialist coexistence, we numerically generated a series of PIPs. To generate the PIPs, we used a simulation with the two plants and the two "resident" herbivores – a specialist ($x = 0$) and a generalist, whose value we varied from 0.5 to 1 by steps of 0.005. We first ran the simulation for 10,000 timesteps to allow the ecological dynamics to reach its final state, which was usually a regular pattern of oscillations in both plant and herbivore abundance. After this, we calculated the fitness of a mutant invading the system, averaged over several cycles. When oscillations were irregular, the fitness was averaged over 10,000 timesteps. The value of x for the mutant was varied from 0.5 – 1. We assumed the mutant biomass was zero, because the mutant is rare.

RESULTS

Most of the results of the timeseries follow the same pattern. At the start of the simulation, when plant abundances are equal, herbivores rapidly branch and evolve towards specialization, because $n > 1$. The interaction between herbivores and plants then generates increasing asynchronous oscillations in plant abundances (Figure 2.1a), changing the fitness landscape and increasing the fitness of generalists (Figure 2.2a-b, solid line). The system temporarily reaches an unstable equilibrium when the herbivores are at the fitness minima, where the trade-off (driving them to specialization) and the oscillations (driving them to generalism) are exactly balanced. The only instance when this does not occur is when n is high enough for the herbivores to completely specialize before the oscillations become strong enough to lead to this intermediate stage.

This intermediate state is known in adaptive dynamics as an evolutionary branching point (Geritz et al. 1998; Waxman and Gavrilets 2005): a strategy that is both convergence stable (so evolution will move towards it) and a fitness minimum, so mutants on either side can invade. If n is not high enough to have two specialists as its only ESS (see below), evolution always proceeds to this state. This is even the case if the herbivores start out as two specialists, or as two specialists and a generalist (results not shown).

Evolutionary branching will eventually take place in either or both of the herbivores, and what follows depends almost entirely on the strength of the trade-off. For low values of n (but still higher than 1) only the more generalist herbivores survive, and the end result is 1 generalist. For high values of n, only the more specialized branches survive, leading to 2 specialists.

The third, and more complicated, result arises for intermediate values of n. In this case, again a single branch of each herbivore survives, such that one herbivore evolves towards further specialization and the other towards a more generalist strategy. Which of the two herbivores becomes the specialist and which the generalist seems random. Eventually the herbivores evolve into one specialist and one generalist, where the specialist feeds exclusively on one plant and the generalist feeds on both, but has a (sometimes slight) preference for the other. The fitness landscape here is asymmetric and shows three maxima, with the herbivores occupying the two lowermost (see Figure 2.2b, dashed line).

At this point, the interaction between herbivore evolution and plant abundances becomes the determining factor in the eventual result. There are seven possible outcomes from here, shown in Figure 2.3. Two of these were expected, as they agree with the results of previous models (two specialists, and two specialists and a generalist), and one is somewhat trivial (extinction of herbivores). The other four, however, are novel outcomes. Two of these occur over almost the entire range for r and T (1 specialist and 1 generalist, Figure 2.3b; 1 specialist and 1 cycling branch, Figure 2.3d). The other two (cycling between 2 specialists and 2 generalists, Figure 2.3g; and complete specialization with generalists repeatedly evolving and

going extinct, Figure 2.3h) are less common, but occur consistently for a part of the range of r and T.

Effect of n

Figure 2.4 shows the simulation results over the entire range for n, for two combinations of r and T ($r = 0.5$ and $r = 1$, $T = 4.5 \cdot 10^6$). For these parameters, all eight possible outcomes occur; the pattern in which they occur over the range of n is representative for most other parameter values.

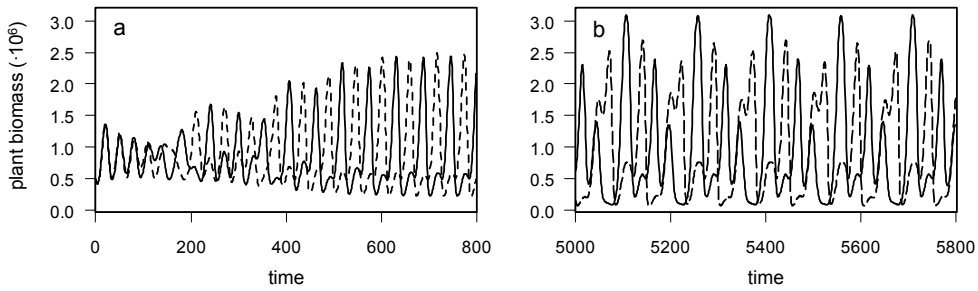

Figure 2.1 Abundance of the two plant species over time, as herbivores become specialized. Solid line: plant 1, dashed line: plant 2. **a** herbivores rapidly evolve partial specialization, ending up at $x_1 \approx 0.28$ and $x_2 \approx 072$ at $t = 1000$; **b** equilibrium state with herbivores at $x_1 = 0$ (completely specialized on plant 2) and $x_2 \approx 0.64$ (mostly specialized on plant 1). The parameters used are $n = 1.3$, $r = 1$, $T = 4.5 \cdot 10^6$; $c_P = 1$; $c_H = 2$; $a = 10^{-5}$; $t_h = 0.1$; $e = 0.25$; $d_P = 0.05$; $d_H = 0.5$

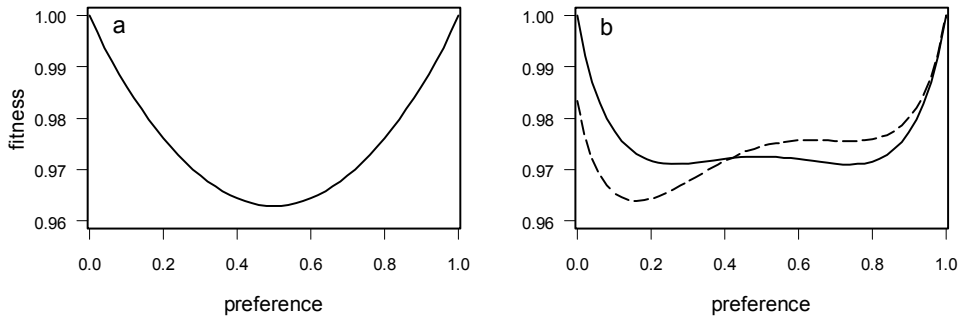

Figure 2.2 Fitness landscapes at different temporal points in the simulation standardized so the highest fitness = 1. **a** $t = 0$, plant abundances are equal, and specialization is favored. **b** solid line: $t = 1000$, oscillations lead to three fitness maxima, two for both specialists and one for the generalist strategy; dashed line: $t = 5000$, interaction between plant abundances and herbivore evolution gradually leads to a skewed fitness landscape with three fitness maxima, where the herbivores occupy the two leftmost maxima.

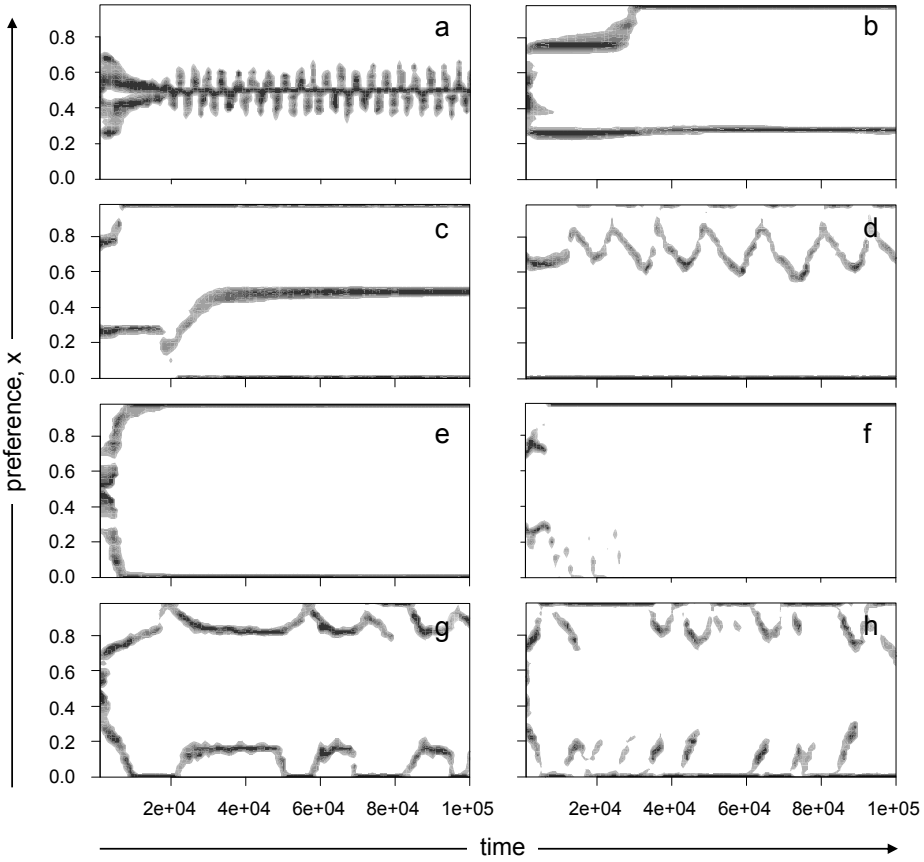

Figure 2.3 The eight possible outcomes. **a**-**f** are the most common ones, occurring over the entire parameter range: **a** 1 generalist (*G*); **b** 1 specialist and 1 partly-specialized generalist (*S*-*G*); **c** 2 specialists and 1 generalist (*S*-*G*-*S*); **d** 1 specialist and 1 cycling branch, with a second specialist repeatedly evolving and going extinct (*S*-*G*/*S*); **e** 2 specialists (*S*-*S*); **f** extinction of herbivores (*E*). **g** and **h** are uncommon but consistent outcomes, found only for the combination of low *r* and intermediate-high *T*: **g** cycling between two specialists and two partly-specialized generalists (*S*-*S*/*G*-*G*); **h** two specialists, with generalists repeatedly evolving and going extinct (*S*-*S*/*G*)

From low to high n, the different outcomes occur in a typical pattern. For low n, the trade-off is not strong enough to favor specialization in the presence of oscillations; the result is one generalist (G). As n increases and specialization becomes possible, the next result is one specialist and one generalist (S-G), followed by the two evolutionary outcomes with three herbivores (two specialists and one generalist (S-G-S), and one specialist with one cycling branch (S-G/S), typically in this order). As n increases even more, the result is only two specialists (S-S), the trade-off being so strong that generalists cannot compete. Increasing n even further eventually leads to the herbivores going extinct (E), for two reasons. First, their dependence on their preferred plant becomes so strong that they cannot survive the

oscillations. Second, eventually the trade-off becomes so strong that the herbivores go extinct before they can specialize.

These six are the outcomes that occur over the entire range for r and T. For a limited range (low r and intermediate-high T), two more outcomes occur (Figure 2.3g-h). These are more uncommon and appear to be limited to this parameter range. In both cases, two complete specialists do evolve; but this is not a stable outcome and more generalist herbivores can invade, resulting in cycles in herbivore evolution. In the first case (*S*-*S*/*G*-*G*, Figure 2.3g), after two specialists evolve, invasion of generalists occurs for both herbivores, until they again end up at the intermediate stage of two partly specialized generalists. From here, they evolve once more into two specialists, repeating the cycle. In the second case (*S*-*S*/*G*, Figure 2.3h), typically occurring for higher n, generalists again invade, often on both sides; but eventually they cannot compete with the specialists and go extinct, after which new generalists can evolve.

These simulation results can for a large part be explained by pairwise invasibility plots (Figure 2.5). These show the course of evolution, assuming the *S*-*G* stage is reached. It is therefore limited to explaining only those cases that pass through this stage as an intermediate step (all except *G* and *S*-*S*, although it still makes clear when *S*-*S* is the only possible ESS). The PIPs show the evolution of the generalist, keeping the specialist fixed at $x = 0$.

For low n, there is an ESS for S-G (Figure 2.5a, 2.5i), with no other singular strategies. As n increases, two additional singular strategies arise: a repeller and, in the case of $r = 1$, an evolutionary branching point (Figure 2.5b). Increasing n first leads to a narrowing of the

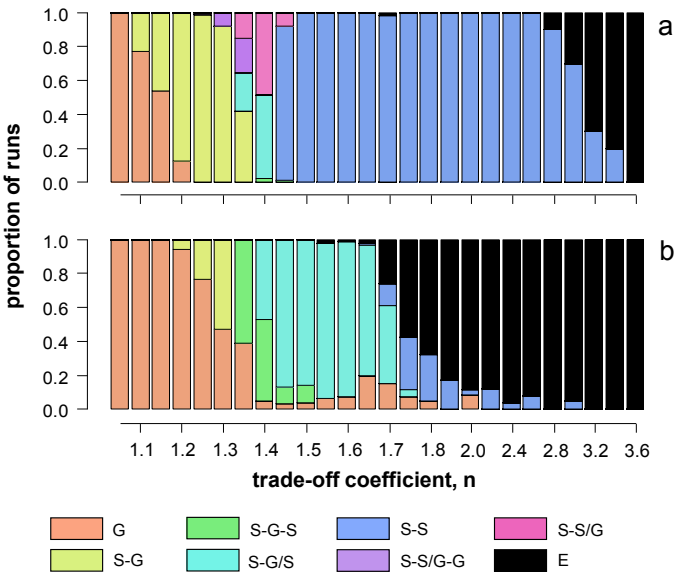

Figure 2.4 Summary of simulation results over a wide range of n, for $T = 4.5 \cdot 10^6$. **a** $r = 0.5$; **b** $r = 1$. Outcomes are as shown in Figure 2.2. Each bar represents at least 100 simulation runs for $1.05 \leq n \leq 2.0$; and at least 10 for $n > 2.0$. Simulations were run for 100,000 time steps, with mutation rate 0.05 and mutation step 0.01. Other parameters are the same as in Figure 2.1

distance to the repeller, making it possible for mutants to cross it; and eventually to loss of the ESS altogether (progression shown in Figure 2.5b-f). In these cases evolution moves towards an evolutionary branching point (as seen in Figure 2.3c-d). What happens after the branching point is reached, is not discernable from the PIP; it can result in stable trimorphism (S-G-S, see Figure 2.3c) or in cycling (S-G/S, Figure 2.3d). In general, the former happens for the lower range of n, and the latter for higher values. Paradoxically, this means that as n increases, the specialist goes extinct in competition with the generalist. A possible explanation for this pattern is that, with increasing n, the resulting interactions between plants and herbivores become stronger, leading to stronger oscillations. This gives the generalist the advantage, allowing it to outcompete the specialist, after which the cycle starts again.

Increasing *n* even more, even the branching point disappears and the system has only one ESS, for *S-S* (Figure 2.5h, 2.5l). In this range only complete specialization can occur; the trade-off is too strong for the generalists to compete with the specialists.

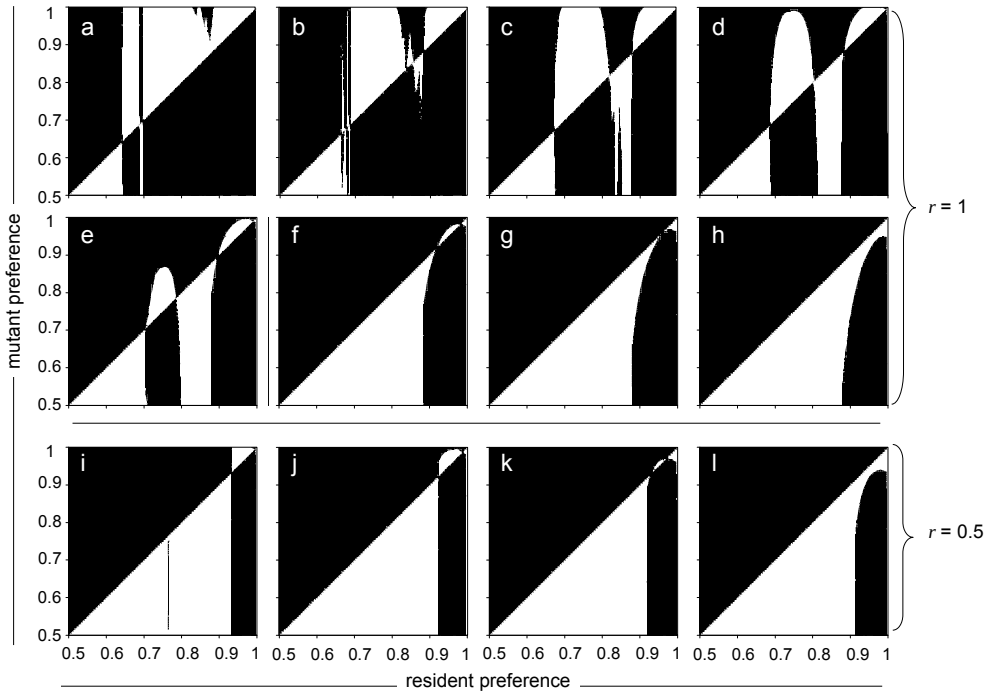

Figure 2.5 PIPs showing the fate of the second herbivore (starting out as generalist) once the S-G stage is reached; 0.5 = generalist, 1 = complete specialization. **a**-**h**: r = 1, all other parameters the same as Figure 2.3. Values for n are 1.3 (**a**) – 1.65 (**h**) by steps of 0.05. **a** ESS with 1 specialist and 1 generalist; **b**-**e**: ESS with 1 specialist and 1 generalist, and branching point. The ESS is unstable in the long run as mutations can jump over the repeller, after which evolution will proceed towards the branching point; **f** branching point only; **g**-**h**: ESS with two specialists. **i**-**l**: r = 0.5. Values for n are 1.3 (**i**)-1.45 (**l**). **i**-**j**: ESS with 1 generalist (though strongly biased towards specializing on the second plant) and 1 specialist; **k** branching point; **l** ESS with two specialists

Figure 2.5j-k give some explanation for what happens with the two less common outcomes (Figure 2.3g-h). Figure 2.5j corresponds to the *S*-*S*/*G*-*G* scenario: there is an *S*-*G* ESS at $x \approx 0.93$, but the distance to the repeller at $x \approx 0.98$ is small enough that mutations can cross it, leading to the *S*-*S* state. At this point, however, the exact same argument holds in reverse: mutations can easily cross the repeller, making it easy for generalists to invade. The herbivores then end up once more at the fitness minima, after which the cycle starts again, leading to the pattern of Figure 2.3g.

Figure 2.5k shows the *S*-*S*/*G* case. Here, there is an evolutionary branching point at $x \approx 0.93$ and an ESS at $x = 1$ (two specialists), a pattern very similar to Figure 2.5f (which leads to *S*-*G*/*S*). The difference is in the value for *r*, which is low and leads to smaller and slower oscillations. This makes it possible for the herbivores to completely specialize rapidly, skipping the intermediate stages described above. When the branching point is approached from below, as when $r = 1$ (and also a significant proportion of the simulations when $r = 0.5$), evolution proceeds as shown in Figure 2.3c-e; but when starting at the extremes, this leads to the pattern shown in Figure 2.3h. This explains why this result is only found for $r < 1$. This argument is supported by the fact that this outcome disappears when mutation rate is decreased, and becomes increasingly frequent with increasing mutation rates. The same is true for the *S*-*S*/*G*-*G* outcome (results not shown).

Effect of *r* and *T*

The general pattern described in the previous section (which evolutionary outcomes are found, and the order in which they occur with increasing values for *n*) largely holds when varying *r* and *T*, two of the parameters most likely to change the plant dynamics, and thereby herbivore evolution. However, changing either *r* or *T* has a distinct effect on which outcomes are most likely to occur. Figure 2.6 shows the results over a narrower range for *n* (1.1-1.8) when *r* and *T* are varied. Several general patterns can be discerned:

First of all, both increasing *r* and increasing *T* tend to result in stronger oscillations, and the total picture is roughly mirrored over the diagonal, with *r* and *T* having more or less equivalent effects. There is, however, also an interaction between the two parameters that makes the picture more complex.

Generalism is most likely to occur when oscillations are very strong – i.e. it becomes more frequent as either growth rate or nutrient availability increases. When both *r* and *T* have high values, generalism eventually becomes the only possible result. Complete specialization (*S*-*S*), on the other hand, is most likely for weak oscillations – when both growth rate and nutrient availability are low.

The most interesting interaction is found in the upper right and lower left corners: low intrinsic growth rate combined with high total nutrients, or high growth rate with low nutrients. These two combinations both give a wide range over which evolution leads to the *S*-*G* outcome. As *r* or *T* (depending on which has the high value) moves further to the extremes, eventually this becomes the only possible outcome apart from *G* and *S*-*S*, and coexistence of

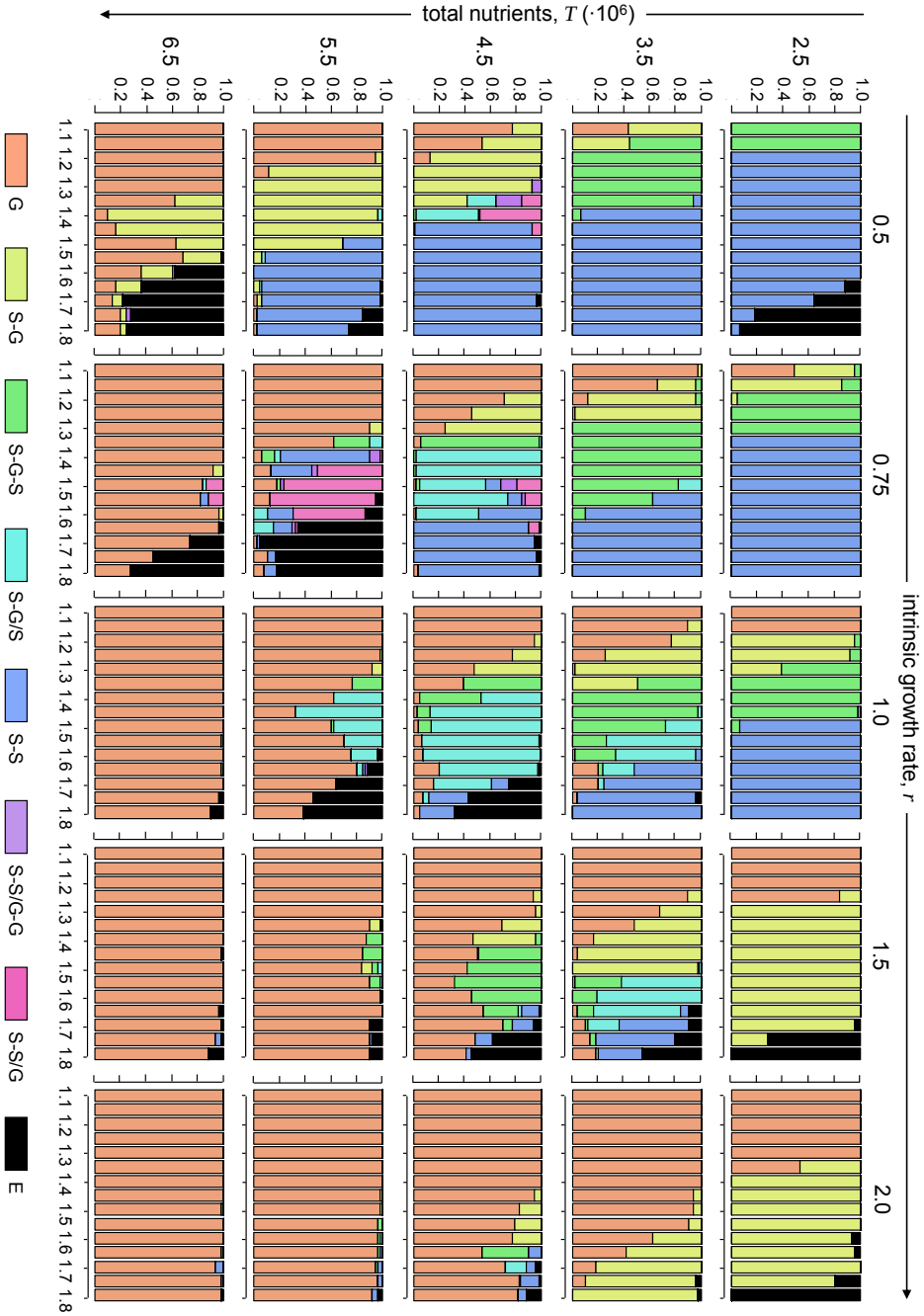

Figure 2.6 Simulation outcomes depending on *n*, *r* and *T*. Each graph has n on the x-axis and the proportion of each outcome on the y-axis; each bar represents at least 50 simulation runs. Parameters are the same as used in Figure 2.1

more than two species becomes impossible. Conversely, coexistence of three herbivores (the two outcomes in 3c-d) is most likely when both *r* and *T* have low to intermediate values.

Finally, extinction usually occurs when the trade-off is strong (high n), and is most frequent under two conditions: first, when both *r* and *T* are very low (Figure 2.6, upper left corner), because eventually plant abundance becomes too low to sustain the herbivore population, and second, when oscillations are very strong – i.e. with increasing *r* and *T* (see Figure 2.7), because the (specialized) herbivores cannot survive the oscillations in their preferred food source. Extinction becomes less likely again when both *r* and *T* are very high, as the oscillations eventually become strong enough that specialists do not evolve at all.

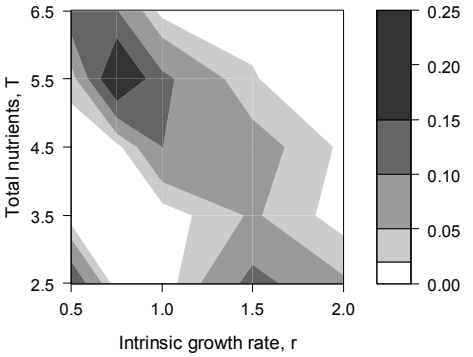

Figure 2.7 Extinction rate as a function of *r* and *T* (extinction rate is the total extinctions for $1.1 \leq n \leq 1.8$)

Robustness of results

The model contains a number of simplifying assumptions. We took a closer look at several factors to determine how sensitive our results are to small changes in the model.

One obvious factor affecting plant dynamics is the shape of the plant growth function. To check whether this changes the results, we redid part of the simulations using several different growth functions. First, we used a ratio-dependent version of the growth function (Arditi and Ginzburg 1989; Abrams and Ginzburg 2000), where the amount of nutrient uptake depends on the available nutrients per unit plant biomass, rather than the absolute amount. The per capita plant growth then takes the following shape:

$$g(F,P_1,P_2) = r\frac{a\left(F(t)/\sum_{i=1}^{N_P}P_i(t)\right)}{b\left(F(t)/\sum_{i=1}^{N_P}P_i(t)\right)+c}, \tag{2.5}$$

which can be simplified to the more intelligible form

$$g(F,P_1,P_2) = r\frac{F(t)}{aF(t)+b\sum_{i=1}^{N_P}P_i(t)}, \tag{2.6}$$

We used values of $a = b = 1$ for the extra parameters. Second, we used a modified version of standard Lotka-Volterra competition, with the difference that the amount of available nutrients takes the place of the carrying capacity:

$$g(F,P_1,P_2) = r\left(1-\frac{\sum_{i=1}^{N_P}P_i}{F(t)}\right). \tag{2.7}$$

Both of these introduce an extra competition term, so that competition is both indirect (through depleting nutrients that the other species needs) and direct (by interfering with the other species' nutrient uptake). The results of both were largely the same as the original version of the model. The same set of evolutionary outcomes occurs, in the same order and pattern over the range of $1.1 \leq n \leq 1.8$. This suggests that it is not the specific growth function that determines the results, but the combination of the trade-off and the effect of competition in itself.

A second issue is the assumption that nutrients are returned to the environment upon death, and immediately become available for uptake. In reality, all dead matter must be decomposed first before the nutrients can be of any use, introducing a time lag in the ecological dynamics. To determine whether this makes a difference, we constructed a version of the model that incorporates such a decomposition stage, which has various effects.

First of all, adding a decomposition stage essentially removes nutrients from the system, as they are caught up in decomposing matter; this effect becomes more pronounced as decomposition rate decreases. This is reflected in the patterns of evolutionary outcomes, which closely resemble those with lower total nutrients. This is not the only effect, however. The amount of nutrients caught in the decomposition stage is dependent on plant and herbivore abundances, and fluctuates over time. Depending on the rest of the ecological dynamics, it can either increase or decrease the amplitude of the oscillations in free nutrients, with consequent effects on plant dynamics. The effect of adding decomposition on herbivore evolution is therefore not straightforward, but it has no qualitative effect on the evolutionary outcomes that can occur.

Evidently, the way we included decomposition is very simplistic. Decomposition does not occur at a fixed rate, but is done by organisms that have their own ecological dynamics; furthermore, we assume dead plant and animal biomass decompose at the same rate, but this is

highly unlikely to be the case. Whether any of this would change the results merits further study.

A third major assumption is that the system is completely closed; the total amount of nutrients is constant, and there is no in- or outflow. We relaxed this assumption in two ways. First, we introduced random variation in the total amount of nutrients. Instead of being constant, at the start of each timestep we drew the value for T from a normal distribution around the basic value (the change in nutrients was added to, or subtracted from, the pool of free nutrients). For the standard deviation we used three different values (10,000, 100,000, and 500,000); only the third caused any significant deviation from the original pattern, and only when either r or T is low (making the effect of the fluctuations relatively more severe). The only significant change is that complete specialization becomes more frequent, and occurs for lower values of n.

Second, we introduced some nutrient inflow and outflow, relaxing the assumption that the system is entirely closed. Inflow was assumed to be constant, whereas the amount of outflow was a proportion of the free nutrients in the system (typically a few per cent or less). The effects of this change are more complicated, and resemble the effects of adding decomposition to the model. This is because the amount of outflow depends on the plant and herbivore dynamics, thereby adding a new level of complexity to the ecological dynamics. But as with decomposition, we find little qualitative difference in the evolutionary outcomes found, provided in- and outflow are low.

Finally, the eventual outcome of evolution depends on the interplay between ecological and evolutionary dynamics; the speed of evolution relative to the ecological dynamics is therefore important. We used a standard "mutation rate" (generation of new lineages) of 0.05, but to see what happens when the speed of evolution is changed, we varied the mutation rate from 0.001-0.1. In general, a lower mutation rate makes generalism more likely, as the herbivores have no time to specialize before the oscillations in plant abundance become prohibitively strong. This effect is most pronounced for high r and high T. Furthermore, the two outcomes limited to low growth rate (see Figure 2.3g-h) disappear altogether if mutation rate becomes very low. Conversely, these two outcomes become more frequent as mutation rate increases. Furthermore, complete specialization (coexistence of only two specialists) is also more likely with high mutation rate, as this means that the herbivores can evolve into specialists before oscillations become very strong. Other than these, the results remain largely the same over the entire range for mutation rate.

DISCUSSION

Our results show that adding nutrient competition to a simple consumer-resource model leads to results that are remarkably more complex than those found by previous models with a similar structure (Egas et al. 2004; Abrams 2006a; Abrams 2006c; Rueffler et al. 2006; Rueffler et al. 2007). Like many previous models we find that a weak trade-off leads to the evolution of a generalist, while a strong trade-off gives rise to two specialists. In addition, like Abrams (2006c), we find that only an intermediate trade-off strength, combined with asynchronous

oscillations in resource abundance, leads to alternative coalitions of consumers. However, in addition to coexistence of two specialists and a generalist, we find four different evolutionary outcomes (plus extinction of herbivores): coexistence of one specialist and a generalist, and three types of cycling between generalist and specialist strategies.

The key factor causing the difference in the results lies in the addition of between-plant competition. While the previous models our work is based on (Abrams 2006a; Abrams 2006c) explicitly look at the effect of endogenous cycles in resources, the effects of between-resource competition are more complicated than that. The extra interaction between the plants, in addition to their interaction through shared herbivores (apparent competition), makes the effect of herbivore evolution on plant abundance far from straightforward. Even without evolution, combining the effects of predation and competition can have more complex results than expected (Kotler and Holt 1989; Chase et al. 2002; Chesson and Kuang 2008). Added to this is the feedback with herbivore evolution, as it is the abundance of plants and the shape (amplitude and period) of their oscillations that drives herbivore evolution. To understand the outcome, it is therefore crucial to take into account the combined effect of all these interactions. For example, the asymmetric fitness landscape in Figure 2.2b is an evolutionary endpoint, with the herbivores occupying the two lowermost maxima. Although it seems obvious from the fitness landscape that, at this point, herbivores close to the third maximum can easily invade, this is not necessarily the case. The simulations and the pairwise invasibility plots (Figure 2.5a, 2.5i) both show that, for relatively low n, this state is in fact an ESS that cannot be invaded by specialists. If a specialist should evolve at this stage, its presence would affect the plant abundances, changing the fitness landscape in such a way that the third maximum would disappear and the new specialist would go extinct. Which types of herbivores can evolve in which coalition of existing ones depends on the interaction between plant growth (r and T) and the trade-off strength, as shown in Figure 2.6.

One recent model (Zu et al. 2011) considers the evolution of predators on competing species; however, the authors find only a limited range of outcomes (a generalist, one specialist, two specialists, or two partly-specialized generalists). Two of these are outcomes we do not find (one specialist and two partly-specialized generalists; the former is simply impossible under the conditions of our model, and the latter we only encountered as an intermediate stage). We believe this difference is probably due to their use of a linear functional response, rather than the more realistic type 2; or alternatively, to the way in which competition is implemented (Lotka-Volterra rather than nutrient competition). Which of these two is the more important factor remains to be seen, but it is certainly an interesting contrast to our own result, and indicates that the role of between-resource competition is far from determined.

Some previous models about specialization have found a broader range of possible outcomes than the three found in Abrams (2006a), but all of these consider two consumer traits co-evolving (coevolution with a behavioral trait, Abrams 2006b; Rueffler et al. 2007; coevolution with dispersal, Kisdi 2002; Nurmi and Parvinen 2011). Our model is the first to give such a diverse set of outcomes for only one evolving trait.

Besides the effect of *n*, the pattern of evolutionary outcomes also depends on the other two parameters studied, *r* and *T*. This is not surprising, given that these two parameters strongly affect plant growth, and in a roughly similar way: higher values lead to oscillations with larger amplitude. This gives a greater advantage to generalists, essentially shifting the pattern of evolutionary outcomes to the right (Figure 2.6); higher values for *n* are required to counteract the effect of the stronger oscillations and lead to the same evolutionary outcome. Conversely, low *r* or *T* leads to small oscillations, thereby shifting the pattern to the left. Thus, we see mostly complete specialization at the upper left corner of Figure 2.6 (*r* and *T* both low), and mostly generalists towards the lower right (*r* and *T* both high). In practice, this would mean that we would expect to find specialists especially in nutrient-poor environments with harsh conditions (low temperature, rainfall, sunlight), whereas generalists would be expected in nutrient-rich environments where conditions are favorable (high temperature, etc.). Whether these predictions of our model hold up is a subject for further study, although one recent review on plant-herbivore interactions and their response to global change (Massad and Dyer 2010) found that increases in temperature, CO_2 and nutrients all increased consumption by generalist herbivores.

In the context of the evolution of generalists and specialists, there is some debate about the most common direction of evolution. Generalists are thought to be more likely to evolve into specialists than vice versa, both because specialists have less opportunity to diversify and because they are more likely than generalists to go extinct. Although phylogenetic studies seemed to confirm the assumption that the transition from generalist to specialist is more likely (Nosil 2002; Stephens and Wiens 2003), later studies have contested these results and concluded that generalists can evolve from specialists (Nosil and Mooers 2005; Stireman 2005).

If a strong trade-off favoring specialists exists, we may indeed expect the evolution of specialists; however, our results clearly show that this is not the whole story. Specialists can stably coexist with generalists (Figure 2.3b, 2.3c); generalists can evolve into specialists and back again (Figure 2.3g); and new specialists may repeatedly evolve and go extinct (Figure 2.3d) while the same may be the case for generalists (Figure 2.3h). There seems to be little reason to assume that evolutionary transitions can occur in one direction only.

Future directions

Although the results of this model are already quite complicated, the model still contains a large number of simplifying assumptions. The most important of these is that the two plants are completely equivalent, both in their interactions with each other and the environment (same growth and death rate, same dependence on nutrients) and their attractiveness and nutritional value to herbivores. We chose to do this because we wanted to focus on the effect of adding nutrient competition on the evolution of herbivores, and chose not to include any other factors possibly affecting the direction of evolution. Furthermore, any differences between plants may affect competition between plants, complicating the results even further and making them difficult to interpret.

This assumption is likely violated in many real systems, and introducing differences between the plants in any of these traits might change the outcome. For example, if the plants have different growth functions, this will likely affect their ecological dynamics, possibly introducing much asymmetry from the start. How this will affect the evolution of the herbivores is unknown; it will probably not be straightforward, and may strongly depend on the kind of differences that are assumed to exist between the plants.

Related to this, our model only looks at evolution from the herbivore's point of view. However, the herbivores are not the only ones facing selective pressure; plants may be expected to evolve ways of coping with herbivory. Moreover, plants face a trade-off between defense against herbivores and competitive ability, especially if defensive strategies (e.g. structural or chemical) are costly (Herms and Mattson 1992), and rapid growth will come at the cost of being preferred by herbivores (Mattson 1980; Moran and Hamilton 1980); for a recent theoretical analysis of plant evolution under this trade-off, see Branco et al. 2010). How this will play out, and interact with the evolution of herbivores, is an open question.

One other limitation is that herbivore preference is entirely fixed. We define preference as the relative attack rate on plant species *i*, or the relative amount of effort the herbivore spends on plant species *i*. The actual amounts a herbivore consumes depends both on its preference and the relative abundances of each plant species; it will consume more of the more abundant plant species, unless it has evolved to be an obligatory specialist ($x = 0$ or $x = 1$). In this sense, actual diet is somewhat flexible and adapts to the circumstances, but there is still little room for adaptive behavior. Previous models have shown (Abrams 2006b; Rueffler et al. 2007; Carnicer et al. 2008) that allowing for adaptive consumer behavior can have a significant effect on the outcome of evolution and coexistence. This could potentially increase the number of evolutionary pathways and endpoints even beyond what we find; alternatively, it could decrease them by stabilizing the cycles found in our results.

Lastly, we introduced competition into the model by using nutrient limitation. While realistic, this is far from the only possible form of interspecific competition. Considering other forms of competition (e.g. over space, light or water), or facilitation (e.g. by preventing soil erosion or water evaporation), in addition to nutrient competition, may give rise to even more complex results.

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Chapter 3

The importance of ecological costs for the evolution of plant defense against herbivory

Ellen van Velzen, Rampal S. Etienne

ABSTRACT

Plant defense against herbivory comes at a cost, which can be either direct (reducing resources available for growth and reproduction) or indirect (through reducing ecological performance). While direct costs have been well studied in theoretical models, ecological costs have received almost no attention. In this study we compare models with a direct trade-off (reduced growth rate) to models with an ecological trade-off (reduced competitive ability), using a combination of adaptive dynamics and simulations. In addition, we study the dependence of the level of defense that can evolve on the type of defense (directly by reducing consumption, or indirectly by inducing herbivore mortality (toxicity)), and on the type of herbivore against which the plant is defending itself (generalists or specialists). We find three major results: First, for both direct and ecological costs, defense only evolves if it the benefit to the plant is direct (through reducing consumption). Second, the type of cost has a major effect on the evolutionary dynamics: direct costs always lead to a single optimal strategy against herbivores, but ecological costs can lead to branching and the coexistence of non-defending and defending plants; however, coexistence is only possible when defending against generalist herbivores. Finally, we find that fast-growing plants invest less than slow-growing plants when defending against generalist herbivores, as predicted by the Resource Availability Hypothesis, but invest more when defending against specialists. Our results clearly show that assumptions about ecological interactions are crucial for understanding the evolution of defense against herbivores.

INTRODUCTION

Plant fitness can be greatly reduced by herbivory, and it is no surprise that a wide variety of defensive strategies have evolved to fend off herbivores. These include physical defenses such as thorns or trichomes, indigestible substances such as cellulose or tannin, or compounds that are toxic to herbivores. Despite the obvious advantage of resisting herbivory, defense comes at a cost (Bergelson and Purrington 1996; Strauss et al. 2002). The most obvious is a cost in allocation: resources invested in defense are unavailable for growth or reproduction (Coley et al. 1985; Coley 1987; Herms and Mattson 1992). Costs can take many other forms, however: from reduced attractiveness to mutualists such as mycorrhizal fungi or pollinators (Gehring and Delph 1999; Strauss et al. 1999; Adler 2000) to increased susceptibility to pathogens (Felton et al. 1999) and lowered competitive ability (van Dam and Baldwin 1998; Kempel et al. 2011). These types of costs, which are only expressed in the context of ecological interactions, are known as ecological costs, in contrast to direct costs (e.g. lower growth rate). Strauss et al. (2002) found a direct trade-off between defense and growth in 51% of the systems studied, whereas ecological costs were present in 62%.

While the evolution of defense in the face of costs has been the subject of theoretical study (Coley et al. 1985; Fagerstrom et al. 1987; Yamamura and Tsuji 1995; Poitrineau et al. 2004; Ito and Sakai 2009), the effect of ecological costs has not received much attention. Most models use a direct trade-off between defense and growth rate (Coley et al. 1985; de Jong 1995; Loeuille et al. 2002; Loeuille and Loreau 2004; Ito and Sakai 2009; Vage et al. 2014) or explicitly allocate resources to various functions including growth and defense (Loreau and de Mazancourt 1999; Krzysztof Janczur 2009; DeAngelis et al. 2012), but do not consider any type of ecological costs. We found one study (Weis and Hochberg 2000) that includes the effect of competitiveness through reduced size, and it reports that including competition has dramatic effects on the outcome of competition between defending and non-defending plants. However, this study only looks at the competitive advantage or disadvantage of defense; it does not study evolutionary dynamics of the defensive trait.

Another commonality of most theoretical studies is that herbivory is often implemented as a constant rate, which is independent of the level of defense, even though there is both theoretical and experimental evidence that defense can affect herbivore population dynamics (Underwood 1999; Underwood and Rausher 2002; Agrawal 2004). Specialist herbivores are especially likely to be affected by the evolution of defense in the plant species they feed on, unlike generalists which may switch to other plant species. This kind of ecological feedback is absent in most models (an exception is DeAngelis et al. 2012), but it may significantly affect evolution.

In this article, we study the evolution of constitutive (i.e. always expressed, not induced) defense against herbivory in the face of either direct or ecological costs. Specifically, in the case of ecological costs, we study a trade-off between defense and competitiveness, rather than between defense and growth rate. We look for conditions leading to either evolutionary stability or evolutionary branching points, allowing for both the evolution of suboptimal (but

stable) strategies and for the evolution of stable polymorphisms. For these purposes, the adaptive dynamics framework (Geritz et al. 1998; Waxman and Gavrilets 2005) is ideally suited. We combine this with simulations to confirm the analysis. Our study looks at three major questions: first, does the trait with which defense trades off (growth rate or competitiveness) affect the evolutionary dynamics of defense? Second, does the type of defense and its effect on herbivory (directly through reducing consumption, or indirectly through toxicity-induced herbivore mortality) influence the level of defense that evolves? And finally, given the above-mentioned possible effect of eco-evolutionary feedbacks, does defense evolve differently against generalist or specialist herbivores?

GENERAL MODEL

We used a set of differential equations to model the ecological dynamics of a single plant and herbivore population. Defense is implemented in two independent traits, each representing a possible effect on the herbivores: x for directly reducing the amount of plant material consumed (for example, by physically interfering with the herbivores), and y for toxicity, causing extra mortality for the herbivores. We used adaptive dynamics to find the ESS solutions for the two traits, and used the differential equations as a basis for a stochastic evolutionary simulation to confirm the results.

1. Ecological dynamics

Plant dynamics

The ecological dynamics of plant abundance $P(t)$, expressed as total plant biomass, is given by

$$\frac{dP}{dt} = f\left(P(t), x(t), y(t)\right) - h\left(x(t), H, P(t)\right). \tag{3.1}$$

Plant growth is given by the first term, $f\left(P(t), x(t), y(t)\right)$. Because including or excluding nutrient dynamics can dramatically affect the ecological and evolutionary dynamics (see e.g. Loeuille et al. 2002), we compared two different plant growth functions, logistic growth or nutrient limited growth; the specifics are described in their respective sections below. The second term in Eq. (3.1) denotes consumption by herbivores (H). This takes the form of a Holling type 2 functional response, modified by the level of defense:

$$h\left(x(t), H, P(t)\right) = g\left(x(t)\right)\frac{HaP(t)}{1 + t_h aP(t)} \tag{3.2}$$

with H being herbivore biomass, and a and t_h the attack rate and handling time, respectively. The effect of defense on consumption is determined by $g(x(t))$, which is assumed to be a decreasing function of $x(t)$:

$$g(x(t)) = \frac{1}{1 + x(t)e_x} \tag{3.3}$$

Here, e_x is the efficiency of defense, or the susceptibility of herbivores to the defensive trait.

We assume toxicity (y) does not directly affect consumption, and its only effect on the level of herbivory is through increasing herbivore mortality. The details are described in the following section.

Herbivore dynamics

To study the effect of an eco-evolutionary feedback between evolution of defense and herbivore population dynamics, we studied two different scenarios for all models, corresponding to specialist or generalist herbivores. Because specialists depend on the focal plant species only, their abundance directly responds to the amount of plant biomass available for their consumption. In contrast, the numerical response of generalist herbivores to plant abundance and level of defense should be much weaker, as they consume more than just the focal plant species and can switch to another food source if the focal species becomes unavailable. We assume that generalist herbivores do not respond numerically to their level of consumption of the plants considered in the model at all, allowing us to assume constant herbivore pressure.

In both scenarios, we assume that herbivores are mobile and can move easily between plants, as is the case for larger herbivores, making the herbivore and plant populations well-mixed and all interactions global.

Generalist herbivores: In this case, we assume herbivore pressure to be independent of plant abundance or the level of direct defense x. We do assume that the level of toxicity y causes increased mortality for generalist herbivores, decreasing herbivore pressure:

$$H = H_{\max} - d_{tox} \tag{3.4}$$

$$d_{tox} = h(x(t), H, P(t))\, y(t) e_y \tag{3.5}$$

where e_y is the parameter determining how toxic any level of secondary compounds is to the herbivores. The total toxicity is determined by the product of the level of toxicity and its effectiveness, $y(t)e_y$, and by the amount of plant biomass consumed, under the assumption that toxic compounds are distributed evenly over the plant material susceptible to consumption.

Specialist herbivores: Here, herbivores are specialized on a plant species and depend on it; a decline in its availability, either due to reduced abundance or increased defense, will affect herbivore abundance. It is in principle possible for the plants to drive the herbivores to extinction. The herbivore dynamics are given by:

$$\frac{dH}{dt} = \varepsilon \frac{c_P}{c_H} h\big(x(t), H(t), P(t)\big) - \big(d_H H(t) + d_{tox}\big), \tag{3.6}$$

where d_H and d_{tox} (see Eq. (3.5)) refer to external mortality and mortality through toxicity, respectively. ε is the conversion efficiency, the fraction of plant biomass converted into herbivore biomass. Finally, c_P and c_H are the conversion factors between nutrients and plant and herbivore biomass, respectively; these parameters are only relevant in the nutrient competition model, but for the purpose of allowing direct comparison between the two models, we chose to use the same equation for herbivore dynamics in both models, including these parameters in the logistic growth model as well. Similarly, we assume that herbivore attack rate and handling time are the same for generalist and specialist herbivores. Although in reality specialists may be more efficient consumers, this allows us to directly compare the results of specialists and generalists.

2. Evolutionary dynamics

Adaptive dynamics

Under the adaptive dynamics framework (Geritz et al. 1998; Waxman and Gavrilets 2005), evolutionary dynamics are assumed to be slower than ecological dynamics, and the fitness of invading mutants is therefore studied assuming that the population is at its ecological equilibrium (evaluating $dP/dt = 0$ (eq. (3.1)) for generalist herbivores, and $dP/dt = 0$ and $dH/dt = 0$ (eq. (3.1) and (3.6)) in the case of specialist herbivores). The fitness of the mutant is defined as its per capita growth rate in a population of residents:

$$W = \frac{1}{P^*} f\left(P^*, \hat{x}, \hat{y}\right) - \frac{1}{1 + \hat{x}e_x} \frac{H^* a}{1 + t_h a P^*} \tag{3.7}$$

where P^* and H^* denote the resident population sizes at ecological equilibrium, and x and y the defense traits of the resident, and $\hat{x}$ and $\hat{y}$ the traits of the mutant. Because the resident growth rate at equilibrium is 0, the mutant can invade if $W > 0$. Evolutionarily singular strategies are found at the points where

$$\left.\frac{\partial W}{\partial \hat{x}}\right|_{\hat{x}=x=x^*} = 0, \left.\frac{\partial W}{\partial \hat{y}}\right|_{\hat{y}=y=y^*} = 0, \tag{3.8}$$

where x^* and y^* denote the evolutionarily singular strategies, which may be ESS strategies, evolutionary repellers or evolutionary branching points. For the equilibrium to be evolutionarily stable (ESS), the following condition must apply:

$$\left.\frac{\partial^2 W}{\partial \hat{x}^2}\right|_{\hat{x}=x=x^*} < 0, \left.\frac{\partial^2 W}{\partial \hat{y}^2}\right|_{\hat{y}=y=y^*} < 0. \tag{3.9}$$

Evolutionary simulations

We used simulations to study the evolutionary dynamics and confirm the robustness of the analysis. The plant population is represented by a number of lineages (typically 200), which can be considered as individual clones in the plant population. The level of defense for each individual lineage is determined by its values for x and y, which are represented as a single genetic value. These trait values determine its growth rate and competitiveness; these in turn determine the ecological dynamics, which follow equations (1-6) above and the functions for plant growth described in the sections below, only substituting the single population P with the whole set of lineages / clones.

Evolution was simulated by the emergence and extinction of lineages (van Velzen and Etienne 2013). Each time step, each lineage has a small probability that mutation will occur (typically $p_{mut} = 0.01$; this probability is the same for all lineages and constant, independent of biomass). When a mutation event occurs, the lineage is split into a mother and daughter lineage. The daughter lineage inherits the trait values of the mother lineage, with some mutation in the trait(s) subject to evolution; if both traits can evolve, one of the two is chosen randomly. The new value for this trait is drawn from a normal distribution around the old value, with a small standard deviation (typically $\sigma = 0.01$). The two traits are thus assumed to evolve independently. When a daughter lineage is created, it takes the place of the lineage with the lowest biomass, which goes extinct; the total number of lineages is kept constant.

Simulations were run for 100,000 time steps, after which the average trait value for the population was recorded.

MODEL 1: DIRECT TRADE-OFF

First, we look at a direct trade-off between defense and growth rate, where the intrinsic growth rate is reduced by investment into defense:

$$r\left(x(t), y(t)\right) = r_{\max}\left(1-(xc_x + yc_y)\right), \tag{3.10}$$

where c_x and c_y are the costliness of the two traits (allowing for the possibility that not all forms of defense are equally costly). Thus there is also implicitly a trade-off between the different defense traits: resources used for one trait are not available for another. The assumptions of all models are summarized in Table 3.1.

For simplicity, we will write r for $r_{\max}$ from this point onwards.

Table 3.1 Assumptions of each of the different trade-offs and plant growth models used.

Model	Plant growth model	Trait affected by trade-off
Model 1: direct cost	Logistic growth (1.1)	intrinsic growth rate (r)
	Nutrient-limited growth (1.2)	intrinsic growth rate (r)
Model 2: ecological cost	Lotka-Volterra competition (2.1)	intraspecific competition coefficient (a)
	Nutrient competition (2.2)	nutrients available for uptake

1.1. Logistic growth

Under the logistic growth model, plant growth takes the form

$$f\left(P(t), x(t), y(t)\right) = r\left(x(t), y(t)\right)\left(1-\frac{P(t)}{K}\right)P(t), \tag{3.11}$$

with K being the carrying capacity of the system. Using this growth function, the fitness function in eq. (3.7) becomes:

$$W = r\left(1-(\hat{x}c_x + \hat{y}c_y)\right)\left(1-\frac{P^*}{K}\right) - \frac{1}{1+\hat{x}e_x}\frac{Ha}{1+t_h aP^*}. \tag{3.12}$$

This equation enables us to derive the fitness gradients for the two traits. It becomes immediately apparent that trait y can never evolve to a nonzero (positive) ESS. Because this trait only indirectly affects consumption by reducing herbivore abundance but has no direct benefits, its fitness gradient is always negative:

(3.13)
$$\frac{\partial W}{\partial \hat{y}} = -rc_y\left(1-\frac{P^*}{K}\right)$$

Because the mutant is rare, herbivore abundance is affected only by the resident values of these traits. This allows for evolutionary cheating: even though toxicity has the positive effect of reducing herbivore pressure, if a nonzero level of toxicity evolves, mutants with a lower investment will have all the benefits of the toxic compounds produced by the resident while carrying none of the costs. This makes $y^* = 0$ the only evolutionarily stable solution. For both generalist and specialist herbivores, simulations show that toxicity can evolve in the short run, but is eventually always replaced by a nondefending strategy; defense is not an evolutionarily stable strategy, even if the costliness of defense is very low (examples of simulation runs are shown in Figure 3.1A-B).

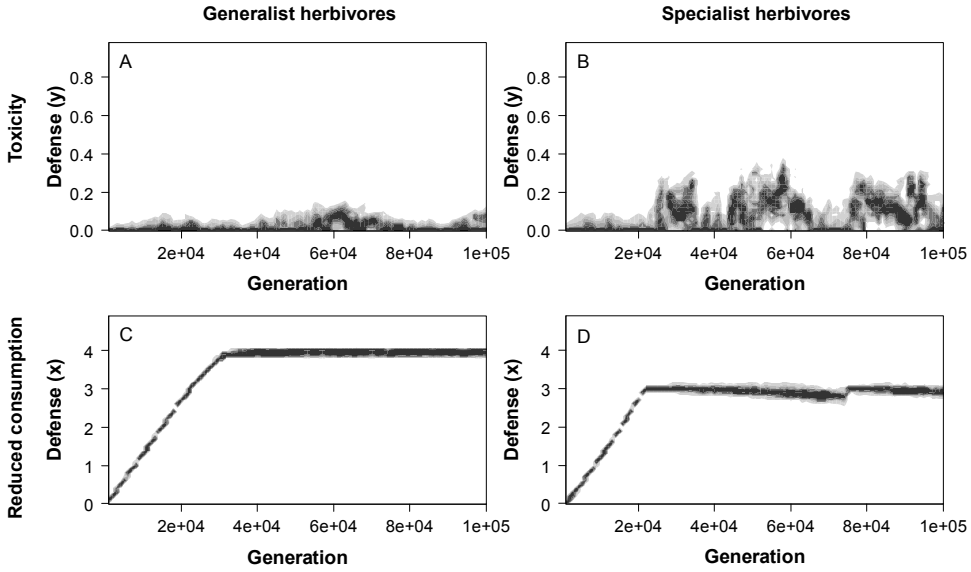

Figure 3.1. Simulations for the evolution of y (toxicity, A-B) and x (reduced consumption, C-D). All scenarios assume logistic growth. Simulations used 200 lineages, mutation rate = 0.01, mutation step size = 0.01; initial values for all lineages for x and y was 0. (see **Evolutionary simulations** for details). Other parameters: r = 0.5, a = 10^{-5}, t_h = 0.1, K = $4{\cdot}10^6$. A, B: e_y = 1.0, c_y = 0.01; C, D: e_x = 0.5, c_x = 0.1. Generalist herbivores (A, C): H = 10000; Specialist herbivores (B, D): d_H = 0.4, ε = 0.25, c_P = 1.0, c_H = 2.0.

The fitness gradient for x has an additional positive term which allows a nonzero ESS:

$$\frac{\partial W}{\partial \hat{x}} = -rc_x\left(1-\frac{P^*}{K}\right)+\frac{e_x}{\left(1+\hat{x}e_x\right)^2}\frac{Ha}{\left(1+t_h aP^*\right)} \tag{3.14}$$

1.1.1. Generalist herbivores (constant)

Substituting the ecological equilibrium for P^* (obtained by setting Eq. (3.1) to 0) and $\hat{x} = x = x^*$, in Eq. (3.14), we get one ESS solution:

$$x^* = \frac{e_x - c_x}{2e_x c_x}. \tag{3.15}$$

The ESS defense depends only on two parameters, the efficiency of defense (e_x) and the costliness (c_x). There is a nonzero investment into defense if $e_x > c_x$, and the ESS investment increases monotonically with e_x to an asymptotic value of $1/2c_x$, if defense is infinitely efficient or costs are infinitely low. Alternatively, it makes sense to express the ESS investment as the fraction of total resources allocated to defense. Multiplying the ESS defense with the cost c_x, we get an ESS investment of

$$x^* c_x = \frac{e_x - c_x}{2e_x} = \frac{1}{2}\left(1-\frac{c_x}{e_x}\right). \tag{3.16}$$

As shown in Figure 3.2A, this increases monotonically with e_x to a maximum value of ½.

1.1.2. Specialist herbivores (dynamic)

The same fitness function and fitness gradients as in the generalist herbivore case apply; the only difference is that H is no longer a constant. Substituting $H = H^*$ (obtained by setting Eq (3.6) to 0) in eq. (3.14), we now find two singular strategies:

$$x^*_{CB} = \frac{e_x - c_x}{2e_x c_x},\ x^*_{NH} = \frac{c_P \varepsilon aK - c_H d\left(1+t_h aK\right)}{c_H e_x d\left(1+t_h aK\right)}. \tag{3.17}$$

The first is the same cost-benefit equilibrium as with constant herbivore pressure (*CB*); the second is the level of defense that reduces the herbivore population to zero (no herbivores,

NH), so that $H^* = 0$, meaning (from eq. (3.14)) that $P^* = K$; this expression can be derived by solving $dH/dt = 0$ (eq. (3.6)) and substituting $P^* = K$.

As Figure 3.2B shows, at the lower range for e_x (low effectiveness of defense compared to the cost) the *CB* equilibrium is lower than the *NH* equilibrium, and vice versa for the higher range of e_x.

Evolutionary stability

For evolutionary stability, Eq. (3.9) must apply. Taking the second derivative of the fitness function with respect to $\hat{x}$:

$$\frac{\partial^2 W}{\partial \hat{x}^2} = -\frac{2e_x^2}{\left(1+\hat{x}e_x\right)^3}\frac{H^* a}{\left(1+t_h a P^*\right)}, \tag{3.18}$$

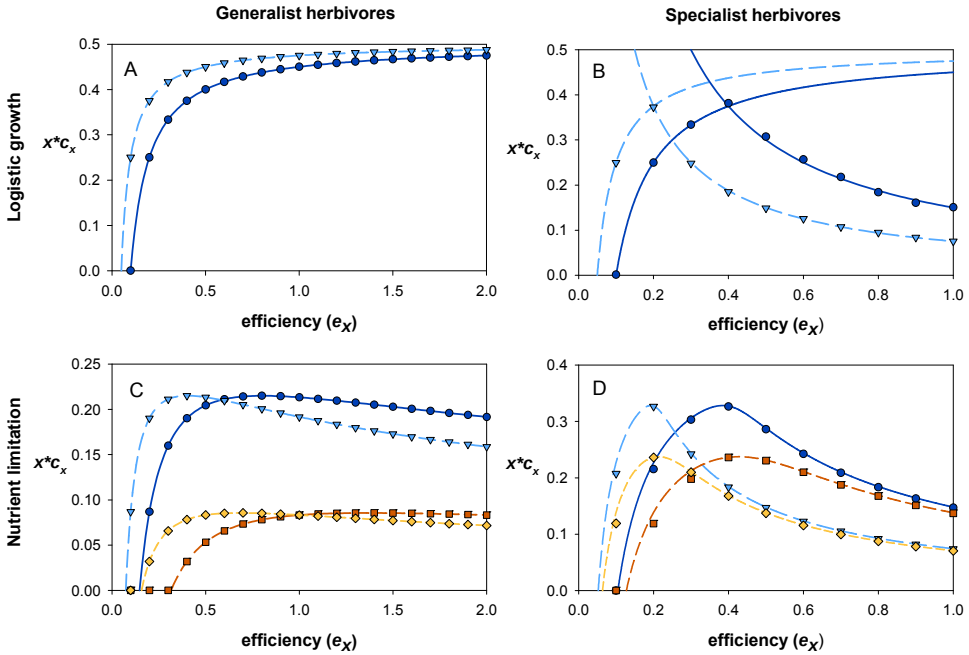

Figure 3.2. Analytical predictions (lines) and simulation results (symbols) for the evolutionarily stable level of defense, expressed as the fraction of resources invested into defense (xc_x). Symbols represent averages of 20 replicate simulations, recorded after 100,000 generations; number of lineages = 200, p_{mut} = 0.01, σ = 0.01. (A, B): logistic growth; solid line, circles: c_x = 0.1; dashed line, triangles: c_x = 0.05. (C, D): nutrient limited growth; solid line, circles: c_x = 0.1, d_p = 0.01; long dash, triangles: c_x = 0.05, d_p = 0.01; medium dash, squares: c_x = 0.1, d_p = 0.05; short dash, diamonds: c_x = 0.05, d_p = 0.05. Generalist herbivores (A, C): H = 10000. Specialist herbivores (B, D): d_H = 0.4, ε = 0.25, c_P = 1.0, c_H = 2.0. In all, r = 0.5, $a = 10^{-5}$, t_h = 0.1, $T = K = k = 4 \cdot 10^6$.

Looking at the first equilibrium (*CB*), we substitute $\hat{x} = x^* = e_x - c_x / 2e_x c_x$ in (3.18), which leaves us with

$$-\frac{16e_x^2 c_x^3}{\left(c_x + e_x\right)^3} \frac{H^* a}{\left(1 + t_h a P^*\right)} < 0. \tag{3.19}$$

Assuming all parameters and P^* are positive, it depends on the value for H^* whether this condition holds. In the model with generalist herbivores, H^* is always positive. The second derivative is thus negative, and the *CB* equilibrium is thus always stable (see Figure 3.1C).

For specialist herbivores, the *CB* ESS is again stable if $x^*_{CB} < x^*_{NH}$ so that $H^* > 0$, but is unstable if $x^*_{CB} > x^*_{NH}$ ($H^* < 0$). x thus always evolves to whichever of the two equilibria has the lowest value. The simulations confirm this (Figure 3.2B). In the *NH* equilibrium, $H^* = 0$; this means the second derivative is always zero, making the equilibrium neutrally stable, meaning that once defense has evolved to this point, all strategies including the ESS strategy have the same fitness and random drift may occur. However, the simulations show this does not happen (Figure 3.1D): as soon as the herbivores reach a very low abundance, there is selection against defense (though it is weak), gradually lowering the average defense in the population. With defense decreasing to slightly lower than the *NH* equilibrium, the herbivores can re-establish, causing a rapid evolution towards the *NH* equilibrium again, after which the cycle repeats.

1.2 Nutrient limited growth

The second model for plant growth, nutrient limitation, takes the following form when assuming a direct trade-off between defense and growth rate (modified from (van Velzen and Etienne 2013):

$$f\left(P(t), x(t), y(t)\right) = \left(r\left(x(t), y(t)\right)\frac{F(t)}{F(t) + k} - d_p\right)P(t). \tag{3.20}$$

In this model plant growth is limited by the amount of nutrients available in the system, following Michaelis-Menten dynamics, where k is the half-saturation constant and $F(t)$ the amount of nutrients available for uptake. $F(t)$ is defined as all nutrients not bound up in plant or animal biomass: $F(t) = T - c_P P(t) - c_H H(t)$, where c_P and c_H refer to the conversion factors between nutrients and plant and herbivore biomass, respectively. T is the total amount of nutrients in the system, similar to K in logistic growth, and d_p is the rate of natural death for plants.

The fitness function for the nutrient limitation model takes the following form:

$$W = r\left(1-(\hat{x}c_x+\hat{y}c_y)\right)\frac{T-c_P P^*-c_H H^*}{T-c_P P^*-c_H H^*+k} - d_p - \frac{1}{1+\hat{x}e_x}\frac{H^* a}{1+t_h a P^*} \quad (3.21)$$

Closed-form solutions of the ESS values can be obtained, but they are not informative except in the extreme case of $d_p = 0$. In this case, the equilibria and their stability are exactly the same as in the logistic growth model. For $d_p > 0$, the ESS values for eq. (3.21) were calculated numerically and are described below; there is always only one single positive ESS value.

1.2.1. Generalist herbivores

The main difference between the logistic growth and nutrient limitation models is that in the model with nutrient limited growth, x^* is no longer a monotonically increasing function of e_x (Figure 3.2C); instead, if the efficiency of defense is very high, the ESS investment drops off again, eventually towards zero if defense is infinitely efficient. The highest investment thus occurs for an intermediate efficiency. While x^* increases more rapidly with e_x if the costliness of defense is lower, again the maximum value for the total investment $x^* c_x$ does not depend on c_x. Numerical analysis and simulations confirm the equilibria are evolutionarily stable (Figure 3.2C).

In contrast with the logistic growth model and the nutrient model with $d_p = 0$, parameters other than the costliness and effectiveness of defense also affect the ESS investment, most notably the plants' natural mortality rate d_p: higher mortality leads to less defense (Figure 3.2C). Nutrient availability also plays an important role: in nutrient-rich systems (high T) investment into defense is less than in nutrient-poor systems. Because higher nutrient availability leads to a higher standing biomass, proportionally less biomass is lost through herbivory, leading to a lower optimal investment. The effects of intrinsic growth rate and resource uptake rate are the same, though much less strongly (Supplementary Material, Appendix A, Figure A1). Lastly, the ESS investment increases with herbivore pressure (H) (Supplementary Material, Appendix A, Figure A2)

1.2.2 Specialist herbivores

ESS investment follows the same general shape as in the logistic growth model, but decreases with plant death rate; only when $d_p = 0$ can the investment evolve to high enough levels that herbivore abundance reaches zero (the NH equilibrium in eq. (3.17)). Numerical calculations and simulations confirm that the equilibria are evolutionarily stable (Figure 3.2D).

Again, nutrient availability has a strong effect on the level of defense that evolves; but in contrast with the model for generalist herbivores, higher nutrient availability (higher T) leads to a higher investment into defense (Figure 3.3B), and the same effect is seen for the other parameters affecting plant growth (intrinsic growth rate r and the half-saturation constant k; Supplementary Material, Figure A1). The explanation for this difference lies in the feedback

between plants and herbivore abundance: the higher plant biomass found in resource-rich habitats causes an increase in herbivore abundance, in turn leading to a higher optimal investment into defense.

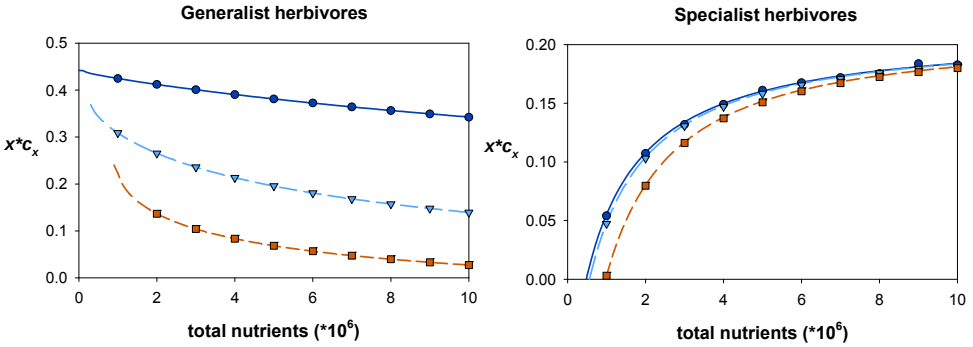

Figure 3.3. Analytical predictions (lines) and simulation results (symbols) for the optimal defense trait value x depending on the total amount of nutrients in the system T. Symbols represent averages of 20 replicate simulations, recorded after 100,000 generations; number of lineages = 200, $p_{mut} = 0.01$, $\sigma = 0.01$. Solid line, circles: $d_p = 0.001$; long dash, triangles: $d_p = 0.01$; medium dash, squares: $d_p = 0.05$. Generalist herbivores (left): $H = 10000$. Specialist herbivores (right): $d_H = 0.4$, $\varepsilon = 0.25$, $c_P = 1.0$, $c_H = 2.0$. In both, $r = 0.5$, $a = 10^{-5}$, $t_h = 0.1$, $k = 4 \cdot 10^6$, $e_x = 1.0$, $c_x = 0.1$.

MODEL 2: ECOLOGICAL TRADE-OFF

2.1 Logistic growth

As an ecological cost, we assume that defense comes with a cost in competitiveness rather than growth rate. This means that growth rate is not affected when a plant is by itself, and the cost is only expressed under competition (see e.g. Kempel et al. 2011). In the logistic growth model, we assume Lotka-Volterra competition where defense negatively affects the competition coefficient:

$$\alpha\left(x(t)\right) = \frac{1}{1 + x(t)c_C}, \tag{3.22}$$

so that investing in defense gives surrounding plants a competitive advantage; for example, if slower growth gives a disadvantage in light competition.

Because adaptive dynamics assumes the mutant biomass is zero, it is not well suited for a model with a trade-off directly affecting competitiveness, as the mutant's competitive effect on the resident will be zero (and thus there will be no costs for the mutant, making $x = \infty$ the only ESS). We adapted the equations to incorporate a nonzero mutant biomass (details of the

derivation of this model can be found in Supplementary Material, Appendix B) and used Lotka-Volterra competition in the simulations. Here we assume that all intra-lineage competition coefficients remain 1, and the inter-lineage competition coefficient is described by eq. (3.22) above. Because the carrying capacity of the system will increase with lower competition coefficients, we normalized competition so that $\bar{\alpha} = \sum_{i=1}^{200} \alpha_i P_i / \sum_{i=1}^{200} P_i = 1$ (see Appendix B).

2.1.1 Generalist herbivores

If costs are low ($c_C \leq e_x$), there is one stable ESS when herbivores are generalist (Figure 3.4A, 3.5A). However, if $c_C > e_x$, the equilibrium value for x^* is no longer evolutionarily stable; instead it is an evolutionary branching point. From here, divergent evolution takes place, leading eventually to one plant population with no defense, and one with a high level of defense. If there are no costs other than in competitiveness, defense evolves indefinitely to higher values in the latter population (Figure 3.5B).

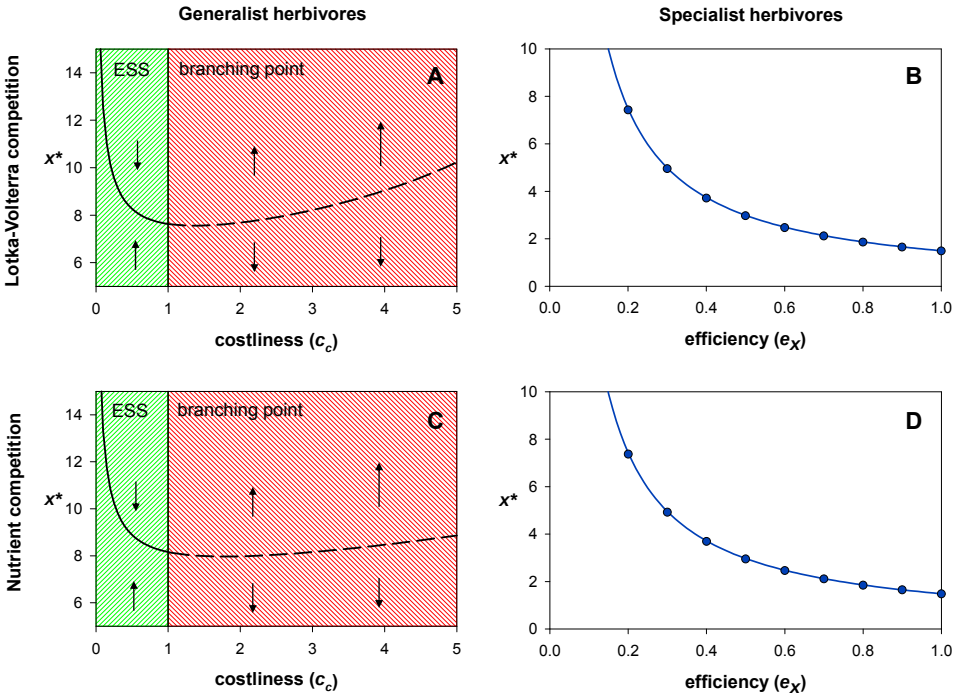

Figure 3.4. Numerical predictions simulation results of the Lotka-Volterra competition model (A, B) and the nutrient competition model (C, D). In all graphs c_X = 0, and mutant biomass = 1/200·P^*, analogous to 1 out of 200 lineages in the simulation (see Supplementary Material, Appendix B). All other parameters the same as in Figure 3.2, unless otherwise specified. Generalist herbivores (A, C): e_x = 1.0. Solid line: stable ESS; dashed line: branching point. Specialist herbivores (B, D): c_C = 1.0. Lines: numerical predictions; symbols: simulation results, average of 10 simulation runs, recorded after 100,000 generations.

If there additional direct costs affecting growth rate as well as competitive ability, it eventually reaches a stable level of investment (Figure 3.5C). If direct costs are high enough that the ESS investment based on that is lower than the evolutionary branching point, no branching occurs and the population reaches a stable ESS (Figure 3.5D).

2.1.2 Specialist herbivores

In the case of specialist herbivores the ESS investment is always nonzero, no matter how high the costliness, unlike for the direct trade-off with growth. When $c_C = 0$, the ESS investment is the amount required to drive the herbivores extinct; when $c_C > 0$, the ESS investment is always lower than this, though the difference is only marginal ($e_x = 1.0$, $c_C = 0$: $x^* = 1.50$; $c_C = 1.0$: $x^* = 1.498$; $c_C = 50.0$: $x^* = 1.497$, all other parameters the same as in Figure 3.2B). Thus, herbivores

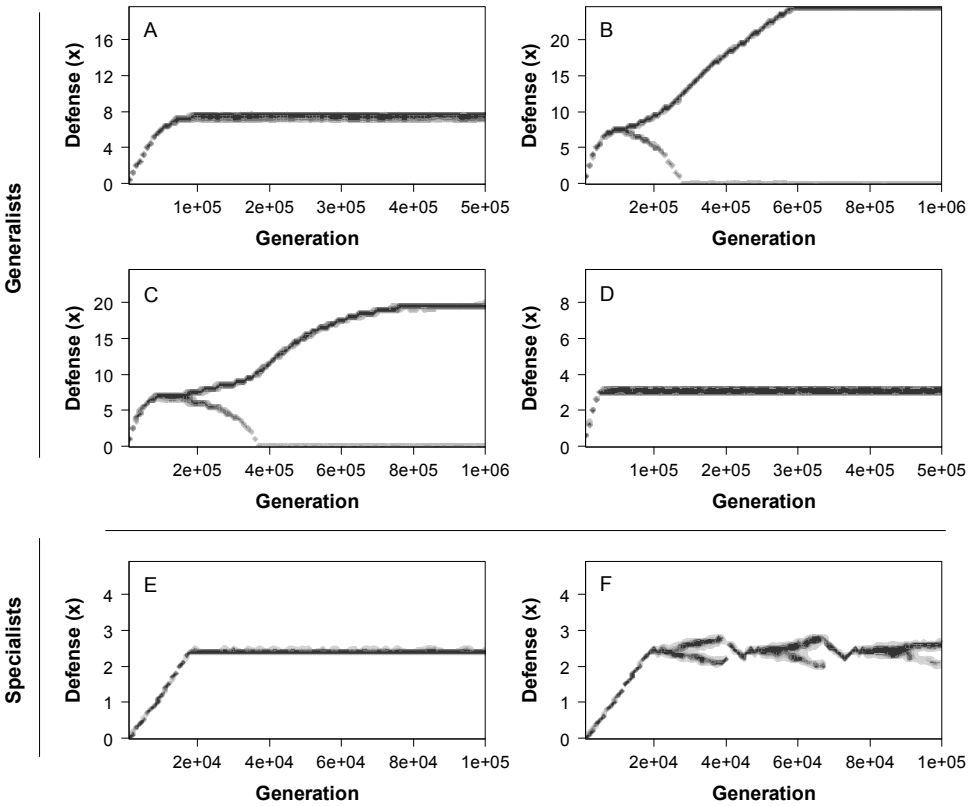

Figure 3.5. Simulations of the Lotka-Volterra competition model with generalist herbivores (A-D) or specialist herbivores (E-F). Number of lineages = 200, mutation rate = 0.01, mutation step size = 0.01; all other parameters the same as in Figure 3.2, unless otherwise specified. (A) $e_x = 1.0$, $c_C = 1.0$, $c_x = 0$; (B) $e_x = 1.0$, $c_C = 2.0$, $c_x = 0$; (C) $e_x = 1.0$, $c_C = 2.0$, $c_x = 0.02$; (D) $e_x = 1.0$, $c_C = 2.0$, $c_x = 0.1$; (E) $e_x = 0.6$, $c_C = 5.0$, $c_x = 0$; (F) $e_x = 0.6$, $c_C = 50.0$, $c_x = 0$.

are always present after the ESS has been reached, though generally in low abundance. However, evolutionary branching does not get off the ground, unless the cost of defense is very high (Figure 3.5E, F), and branching never leads to stable coexistence of defended and undefended plants. Though initially branching may occur, especially when the efficiency of defense e_x is low, the feedback between ecological and evolutionary dynamics prevents stable coexistence of two defense strategies. As plants with a lower investment in defense evolve, total consumption by herbivores increases, leading to higher herbivore abundance. The increase in herbivore pressure drives the less-defending population extinct, after which the more-defending population returns to the ESS value (Figure 3.5F). Thus, in contrast to the model with generalist herbivores, stable branching and coexistence of different trait values never occurs with specialist herbivores. Increasing the mutational step size or starting the simulation with a diversified plant population does not change this: the presence of a less-defended plant invariably causes a rise in herbivore pressure, driving the less-defended plant extinct.

2.2 Nutrient competition

We modified the nutrient limitation model into a model for nutrient competition, including a cost in competitiveness rather than growth rate. In this case, we assume that investment into defense reduces the ability to monopolize nutrients, so that competitors with lower defense get a disproportionally larger share. Thus, the amount of nutrients that is available to a plant P_i depends, apart from total plant and herbivore biomass, on its own level of defense as well as that of its competitors:

$$f\left(P_i(t), x(t)\right) = P_i(t)\left(r\frac{F_i(t)}{F_i(t)+T} - d_p\right)$$
$$F_i(t) = T - c_P\sum_{j=1}^{j_{max}}\alpha_j P_j(t) - c_H H(t) \qquad (3.23)$$

The competitiveness $\alpha(x)$ is again given by the decreasing function of x given in Eq. (3.22), and the values are again normalized so that $\sum_{i=1}^{200}\alpha_i P_i / \sum_{i=1}^{200} P_i = 1$.

2.2.1 Generalist herbivores

The results for generalist herbivores mirror the results of the Lotka-Volterra model (compare Figure 3.4C with Figure 3.4A). Low cost ($c_C \leq e_x$) again gives rise to a stable ESS, but when $c_C > e_x$ the equilibrium is an evolutionary branching point. From here, the defense trait diverges into a defending and a non-defending strategy.

2.2.2 Specialist herbivores

As in the Lotka-Volterra model, ESS investment for specialist herbivores decreases with efficiency e_x, and again only marginally decreases with c_C (Figure 3.4D). Evolutionary dynamics

around the ESS are the same as in the Lotka-Volterra model: while initially branching may occur, stable coexistence is not possible.

DISCUSSION

Our results show that the type of trade-off (direct vs. ecological) between herbivore defense and other plant traits can have a dramatic effect on the course of evolution. In addition, generalist herbivores can cause very different evolutionary dynamics in plants than specialists.

Direct and ecological trade-offs

Growth rate and competitive ability are often used interchangeably when it comes to trade-offs between defense and competition, but the distinction between the two is not trivial. While a plant's growth rate is obviously a major factor determining its ability to compete with other plants, there is a major difference between a trade-off affecting competitive ability through growth rate and a trade-off directly affecting competitive ability itself. While many models exist that study the evolution of defense when defense is costly, ranging from relatively simple models (Coley et al. 1985; Fagerstrom et al. 1987; Yamamura and Tsuji 1995; Poitrineau et al. 2004; Ito and Sakai 2009) to community or metacommunity models (Loeuille et al. 2002; Loeuille and Loreau 2004; Loeuille and Leibold 2008; Vage et al. 2014), all these models use a trade-off with growth rate or resource uptake rate. To our knowledge, our model is the first to look at a trade-off affecting competitive ability itself, and our results show that this has a major impact on the resulting evolutionary dynamics.

Direct effects always lead to one optimal strategy against herbivores. In addition we found, as did Loeuille et al (2002), that including nutrient dynamics had several major effects on the evolutionary dynamics, especially when defense is against generalist herbivores. In a logistic growth model with direct costs the ESS investment always increases with increased efficiency of defense, and solely depends on the cost and efficiency of defense. In contrast, in the nutrient limitation model, the highest investment occurs for intermediate efficiency; moreover, ESS investment depends strongly on other parameters determining plant growth, especially nutrient availability (see **The resource availability hypothesis** below). While throughout the manuscript we have assumed a direct trade-off to be between defense and the intrinsic growth rate r, this is not the only direct trade-off possible in the nutrient limitation model. Assuming instead that the trade-off affects nutrient uptake rate (where higher defense increases the half-saturation constant k) or natural mortality (increasing d_p) does not significantly change the results (Supplementary Material, Appendix A, Figure A3). In all cases, a single ESS is found, with the highest investment occurring for intermediate efficiency.

However, when the trade-off affects competitive ability (intraspecific competition or ability to utilize shared nutrients), high costs can lead to evolutionary branching and stable coexistence of non-defending and defending plants. Like Weis & Hochberg (2000), we find that allowing for the possibility of asymmetric competition (through a trade-off with competitiveness) leads to dramatically different predictions on optimal defense. Unlike their

study, however, we also looked at the effects of a trade-off between defense and competitiveness, and our results indicate that this can lead to divergent evolution and the coexistence of different strategies. Therefore, it is possible for plants to have no defense against herbivory, even if faced with conditions where defense would seem an optimal strategy.

Other mechanisms have been found to lead to stable coexistence of different defense strategies; examples include selective grazing by herbivores, combined with a higher nutrient content of preferred plants (Branco et al. 2010), dispersal and metacommunity dynamics (Loeuille and Leibold 2008) and the existence of a nonlinear (concave) trade-off between growth and defense (Vage et al. 2014). While we assume a linear trade-off between defense and growth in Model 1, relaxing this assumption does not change our main result that there is only one stable ESS (Supplementary Material, Appendix A, Figure A4). Our model adds a new mechanism for evolutionary divergence and coexistence, finding both are possible in a relatively simple ecological model. However, this result only applies to generalist herbivores; with specialist herbivores, although different strategies may evolve to some extent, it is never possible for them to stably coexist. This is because of the feedback between plant defense and herbivore population dynamics: when a non-defending plant arises, whether through gradual evolution or immigration, the increased food availability increases herbivore abundance, to which the non-defending plants is defenseless. Not only are assumptions regarding which traits are affected by the trade-off critical for predicting the outcome of evolution, so are the assumptions on how the herbivores respond to the evolution of defense.

Direct and indirect effects of defense

We find that herbivore defense can only evolve if it has a direct effect on the consumption rate. Defense working indirectly through affecting herbivore pressure, such as the presence of toxic compounds in consumed plant material, does not evolve. A population producing toxic defense compounds is open to evolutionary cheating: a mutant with a lower investment into defense has a negative effect on itself (through increased herbivore pressure), but equally on its competitors, yielding no overall negative fitness effects; but it does give the advantage of economizing on defense. If toxicity confers any cost at all, even a very low cost, this strategy always has a higher fitness, and in none of our scenarios could pure toxicity evolve. The same reasoning applies to other forms of defense that work only through indirect means, such as compounds that lower digestibility of consumed plant material: these would not evolve either. A positive direct effect on the mutant is necessary for defense to evolve.

Both toxicity and low quality can evolve as defense, if they also directly reduce consumption of the defending plant. We assume that the effect of toxicity is always indirect, as herbivores in our model are mobile and can move freely through the plant population; this is not always the case in nature, where small arthropod herbivores spend their entire lifespan on the same plants, allowing toxicity to affect consumption through reducing the local herbivore population affecting it (but not the surrounding competing plants). This scenario is more akin to a direct positive fitness effect and may allow pure toxicity to evolve.

A similar argument can be made for low digestibility. Lower quality food can reduce herbivore growth rate and increase their mortality (Häggström and Larsson 1995; Benrey and Denno 1997; Coley et al. 2006), but this only has an effect on plant evolution if low quality food also reduces consumption rate, for example because it takes longer to pass through the digestive system (Clissold et al. 2009). Another way that toxicity or low quality can directly reduce damage is if herbivores learn to recognize and avoid them. Intuitively, this appears most likely with generalist herbivores, which have the option of easily switching to other plant species.

The resource availability hypothesis

The resource availability hypothesis states that slow-growing plants in resource-poor environments should invest more into defense than fast-growing plants in resource-rich environments (Coley et al. 1985; de Jong 1995). While it has been argued that this is not necessarily the case if the plants affect the amount of resources available (Loreau and de Mazancourt 1999), it has empirically been confirmed (Endara and Coley 2011).

In our model, we found two opposite predictions for the effect of nutrients and intrinsic growth rate, driven by the fact that faster-growing plants have a higher standing biomass. If herbivores do not respond numerically to plant biomass (the generalist scenario), this means that the plants' per capita loss to herbivory is lower. Consumption does increase with plant biomass, but not proportionately, leading to a lower optimal level of defense. By contrast, if herbivores become more abundant when they have more food available (the specialist scenario), faster-growing plants should invest more into defense.

External or natural mortality rate correlated negatively with optimal defense across all scenarios. This can be understood as follows: if plant material can be lost either through natural mortality or through herbivory, higher natural mortality decreases the probability that the loss will occur through herbivory, making defense less optimal even if the total loss through herbivory is the same. This contradicts the RAH, which states that slow-growing plants should defend more because lost biomass is more difficult to replace. Because slow-growing plants tend to have slower turnover, the effects of faster growth and higher mortality may be difficult to disentangle, but our result dovetails nicely with studies showing that defense is reduced in ageing leaves (van Dam et al. 1994; Iwasa et al. 1996; van Dam et al. 1996).

Future directions

Our model does not allow for inducible defense, instead assuming that all defense is constitutive. If defense is costly or herbivore pressure is low, inducible defense may confer a fitness advantage over constitutive defense, because defenses only have to be mobilized when needed, reducing costs of defense (Poitrineau et al. 2004; Tiffin et al. 2006; Ito and Sakai 2009). Moreover, inducible and constitutive defenses have different effects on herbivore population dynamics (Underwood and Rausher 2002): constitutive defense has a stronger negative effect on herbivore abundance than inducible defense, which may again affect optimal defense.

Furthermore, we divided the scenarios between generalist and specialist herbivores, assuming plant suffer only one of the two, while in nature they would likely face both. Generalist and specialist herbivores may exert very different selection pressures (Lankau 2007): defenses that work against generalists are ineffective against specialists that have co-evolved with the plant, and the same trait that confers resistance against generalist herbivores can increase susceptibility to specialists. This may allow for polymorphism in defense (Agrawal et al. 1999), and generate more complicated evolutionary dynamics.

Lastly, throughout our study we assume herbivores easily move from plant to plant; this assumption likely affects some of our conclusions (especially our results on direct vs. indirect effects). A model structure allowing for localized effects may give different results: in particular, it may allow for toxicity to evolve where in our model it does not. It is unclear whether it would change the overall conclusions that direct (growth) costs always give rise to one stable ESS but a competitiveness cost can lead to coexistence; the metacommunity model by Loeuille & Leibold (2008) would suggest that divergent strategies can evolve under direct costs as well. We believe this would be the most interesting avenue for further research.

In conclusion, ecological costs and the role of ecological interactions in the evolution of herbivore defense have been largely ignored in theoretical studies so far. Our results suggest that competitive effects can have a dramatic effect on the course of evolution.

Chapter 4

The role of within-host competition in coexistence in multiparasitoid-host systems

Ellen van Velzen, Rampal S. Etienne

ABSTRACT

Multiparasitism (females of multiple species parasitizing the same host) is a ubiquitous phenomenon in parasitoids, yet the role of within-host competition has been mostly ignored in multiparasitoid-host models. Here we study the effects of interspecific between-adult and within-host competition on parasitoid coexistence. We adapt a Nicholson-Bailey model to allow for varying levels of both between-adult competition (varying the overlap in species distributions) and within-host competition (varying the number of offspring that can successfully emerge from the same host). We find that stronger between-adult competition reduces the probability of coexistence, while surprisingly, stronger within-host competition promotes it. Asymmetric between-adult competition (a fecundity difference between the two species) reduces the opportunities for coexistence when compared to symmetric competition; this can be counteracted by asymmetric within-host competition (within-host competitive advantage of the lower-fecundity species), but only when within-host competition is strong and the correlation between the parasitoids' distributions is not too weak or too strong. We discuss our results in the context of the interaction between two parasitoid species, *Nasonia vitripennis* and *N. giraulti*, which have strongly correlated distributions and high levels of multiparasitism in the field. We conclude that either low or asymmetric within-host competition are unlikely to explain their coexistence.

INTRODUCTION

To maximize their fitness, female parasitoids must choose their hosts in such a way that they maximize their offspring's success (optimal oviposition theory, Jaenike 1978). In general, the optimal oviposition strategy is to exploit a host by herself, so her offspring will not have to share resources with competitors (Godfray 1994; van Baaren et al. 1994; Crespo and Castelo 2009). However, superparasitism (parasitizing a host already used by a conspecific female) can be an adaptive strategy (Charnov and Skinner 1984; van Alphen and Visser 1990; van Alphen et al. 1992), for example when hosts are scarce and searching for unparasitized hosts would be inefficient. Superparasitism is indeed frequently found in nature (van Alphen and Visser 1990; Godfray 1994; Dorn and Beckage 2007), and intraspecific host sharing (offspring of multiple females emerging from a single host) is ubiquitous in gregarious species.

In contrast, interspecific host sharing is very rare (reviewed in Harvey et al. 2013). Multiparasitism (parasitizing a host already used by a heterospecific female) is adaptive only under two scenarios: if the offspring of one parasitoid do not consume the entire host or do not require the entire host to develop (Miller 1982; Magdaraog et al. 2012), or if the multiparasitizing female has a competitive advantage over the first. The latter is the rule: one species wins within-host competition, and a range of mechanisms for eliminating competitors have been found in species faced with interspecific within-host competition (see e.g. Fisher 1963; Hagvar 1988; Chau and Maeto 2008; Harvey et al. 2013). So while multiparasitism is common, it rarely leads to interspecific host sharing.

Perhaps because interspecific host sharing is so rare, it has received relatively little attention in theoretical studies. Most multiparasitoid-host models assume either that one species always arrives first and the second species does not multiparasitize, or that one species is always competitively superior (May and Hassell 1981; Kakehashi et al. 1984; Klopfer and Ives 1997; Porter and Hawkins 2003; Lane et al. 2006; Kon and Schreiber 2009). In some other models the outcome of multiparasitism is decided by who arrives first (Hogarth and Diamond 1984; Hackett-Jones et al. 2009). Most of these models consider solitary parasitoids, in which complete competitive superiority is a reasonable assumption; but even the models that do include gregarious parasitoids (Klopfer and Ives 1997; Lane et al. 2006; Kon and Schreiber 2009) do not include the possibility for host sharing. Only one study explicitly looks at the effect of within-host competition on coexistence in solitary parasitoids (Hogarth and Diamond 1984), and finds that the competitive superiority of either species has negligible effect on the likelihood of coexistence. However, this model may be too simplistic, incorporating the probability to win within-host competition as a constant that does not depend on the abundances of the two parasitoid species. This may be appropriate when considering solitary parasitoids, but in gregarious parasitoids for which superparasitism and host sharing are common, the abundances of the two species (and therefore their encounter rates with the hosts) should be incorporated into how within-host competition plays out. Hence, a proper model for multiparasitism and its effects on coexistence is still lacking. Our aim in this study is twofold: first, to develop a model for gregarious parasitoids to study the effect of

multiparasitism more closely; and second, to apply this new model to understand the coexistence of two closely related parasitoid species, *Nasonia vitripennis* and *N. giraulti*, which we will introduce in the next section. We develop the model with this system in mind, but the results are applicable to multiparasitoid-host systems in general.

The *Nasonia* system

Nasonia are a genus of gregarious parasitoid wasp species, laying several eggs in one host. They are the main parasitoids of *Protocalliphora* spp., which in turn parasitize young birds. In the field they are collected from birds' nests. Individuals mate at emergence on the natal patch (including sib-mating) and females then disperse to find suitable hosts (Whiting 1967). Four species have been described in this genus, of which three have a limited geographical distribution: *Nasonia longicornis* in Western North America, and *N. giraulti* and *N. oneida* occurring sympatrically in Eastern North America. They all co-occur with the fourth species, *N. vitripennis*, which has a worldwide distribution (Darling and Werren 1990).

We illustrate our model with *N. vitripennis* and *N. giraulti*, because their coexistence is puzzling. *N. giraulti* has a lower attack efficiency and a longer handling time per host (pers. obs.) and lays fewer eggs per host (Grillenberger et al. 2009). Yet despite its obvious inferiority, it has not been competitively excluded, although its abundance in the field is much lower than that of *N. vitripennis* (Grillenberger et al. 2009). Competing parasitoids may coexist even when one parasitoid is objectively an inferior competitor, but this requires that interspecific aggregation is weak (Ives 1988a; Ives 1988b; Hartley and Shorrocks 2002). This is certainly not the case for the interaction between *N. vitripennis* and *N. giraulti* because in the field *N. giraulti* is always found together in the same nest with *N. vitripennis*, and host sharing between the two species is common (Grillenberger et al. 2009). It is clear that within-host competition affects fitness: offspring body size is determined by nutrient availability during development, with overcrowding causing smaller offspring (Rivero and West 2005; Sykes et al. 2007), and body size is correlated with longevity as well as fecundity in *N. vitripennis* (Flanagan et al. 1998; Rivero and West 2002; Sykes et al. 2007). Furthermore, interspecific host sharing confers the added disadvantage that offspring of a competitor of a different species are not available for mating, as is the case with superparasitism. Not only are there fewer suitable mates available, but time and energy is wasted by courting and mating with the wrong species, which cannot lead to viable offspring due to incompatibility caused by *Wolbachia* bacteria (Breeuwer and Werren 1990).

Superparasitism is common in all *Nasonia* species, but multiparasitism is rare between *N. vitripennis* and *N. longicornis*, and experimental evidence shows both species avoid multiparasitism more strongly than superparasitism (Ivens et al. 2009). In contrast, multiparasitism rates between *N. vitripennis* and *N. giraulti* in the field are high (Grillenberger et al. 2009). Even more surprisingly, a host choice experiment suggests that *N. giraulti* prefers multiparasitizing over parasitizing an empty host (Pérez-Vila et al, in revision), which seems to directly contradict optimal oviposition theory. This suggests that multiparasitizing may confer an advantage to *N. giraulti*, and this could potentially explain its persistence in competition with

N. vitripennis. While little information is available about the relative competitive abilities of the two species within the host, the high incidence of multiparasitism and host sharing alone makes the effect of within-host competition on coexistence worth investigating.

We extend a standard Nicholson-Bailey model for host-parasitoid interactions in discrete time to two parasitoid species with correlated distributions, and combine this with individual-based simulations to study the effects of between-adult and within-host competition more closely. We then discuss what these results mean for the coexistence of *N. vitripennis* and *N. giraulti*. Specifically, we ask whether we can explain the persistence of *N. giraulti* in the face of competition with a superior competitor, with two of the three mechanisms described above. First lowered within-host competition, while not giving an advantage to multiparasitism per se, may explain why *N. giraulti* is not outcompeted by *N. vitripennis* in the field. Second, an advantage in within-host competition may allow *N. giraulti* to compensate for its competitive disadvantage in other life history traits; this would confer an advantage to multiparasitizing, as this competitive advantage is limited to multiparasitized hosts. Thus, the former mechanism may explain the persistence of *N. giraulti* only, whereas the latter may additionally explain its preference for multiparasitizing.

METHODS

Our model is based on the standard Nicholson-Bailey host-parasitoid model for a single host and parasitoid (Nicholson and Bailey 1935), extended to two gregarious parasitoids with correlated distributions, and assuming that offspring of both parasitoid species can emerge from a multiparasitized host. The basic model takes the following form:

$$\begin{aligned} H_{t+1} &= \lambda H_t \cdot f\left(V_t, G_t\right) \cdot e^{-dH_t} \\ V_{t+1} &= c_V H_t \left(g_V + p_V g_{VG}\right) \\ G_{t+1} &= c_G H_t \left(g_G + p_G g_{VG}\right) \end{aligned} \tag{4.1}$$

Here, H_t, V_t and G_t stand for the number of hosts and parasitoids at time t, where V and G can be interpreted as *N. vitripennis* and *N. giraulti*, respectively. λ is the intrinsic growth rate of hosts that escape parasitism, d is density dependence of the hosts, and c_V and c_G give the fecundity of the parasitoids V and G. g_V, g_G and g_{VG} denote the fractions of hosts parasitized by only V, only G, or both. p_V and p_G give the fraction of V and G in the offspring that emerge from multiparasitized hosts. Finally, $f\left(V_t, G_t\right)$ is the escape function, the fraction of hosts that escape parasitism by both species.

The escape function in a single parasitoid-host model is generally assumed to follow the negative binomial distribution. This assumes hosts are found in patches; parasitoids are distributed among the patches, after which they search randomly within the patch (May 1978). This is a good approximation for *Nasonia* wasps, which parasitize the pupae of flies in animal carcasses and birds' nests, and rarely find a second patch with hosts to parasitize (Grillenberger et al. 2008), Because we are studying a system of two parasitoids with correlated distributions,

we used a bivariate negative binomial distribution (Ives 1988b; Klopfer and Ives 1997), which has the following escape function:

$$f\left(V_t, G_t\right) = \left(\left(1 + \frac{a_V V_t}{k}\right)\left(1 + \frac{a_G G_t}{k}\right) - r\frac{a_V V_t a_G G_t}{k^2}\right)^{-k}. \tag{4.2}$$

Here a_V and a_G represent the two species' respective search efficiencies, and k is the clumping parameter determining the degree of spatial aggregation of the hosts, and thereby the aggregation of encounters between hosts and parasitoids. If $k = \infty$, the negative binomial distribution reduces to a Poisson distribution (reflecting a lack of spatial aggregation in the hosts), and lower values of k denote stronger aggregation. The host-parasitoid dynamics are stable when $k \leq 1$ (May 1978). Finally, r is the correlation between the distributions of the two parasitoids among the patches. A positive value for r denotes positive correlation in patch sharing between the two species, either because of interspecific attraction, or because both species use the same cues to find a patch. Conversely, a negative value indicates interspecific avoidance.

Even if the distributions of the two species over the patches are strongly overlapping (high r), this does not necessarily mean they share the same hosts within those patches. The covariance per host between the number of encounters of each species (number of hosts parasitized by each species), ϱ, is given by

$$\rho = r\left(1 + \frac{k}{a_V V_t}\right)^{-1/2}\left(1 + \frac{k}{a_G G_t}\right)^{-1/2}, \tag{4.3}$$

which decreases with k (so stronger aggregation leads to a higher covariance), and increases with the mean number of encounters for both species ($a_V V_g$ and $a_G G_g$, respectively).

Calculating the fractions g_V, g_G and g_{VG} is fairly straightforward. Because the total fraction of hosts encountered per species follows a negative binomial distribution, it follows that

$$\begin{aligned} g_V + g_{VG} &= 1 - \left(1 + \frac{a_V V_t}{k}\right)^{-k} \\ g_G + g_{VG} &= 1 - \left(1 + \frac{a_G G_t}{k}\right)^{-k} \end{aligned} \tag{4.4}$$

Because $g_V + g_G + g_{VG} + f\left(V_t, G_t\right) = 1$, the fraction g_{VG} can be derived from equations (4.2) and (4.4):

$$(4.5)\ g_{VG} = 1 - \left(1 + \frac{a_V V_t}{k}\right)^{-k} - \left(1 + \frac{a_G G_t}{k}\right)^{-k} + \left(\left(1 + \frac{a_V V_t}{k}\right)\left(1 + \frac{a_G G_t}{k}\right) - r\frac{a_V V_t a_G G_t}{k^2}\right)^{-k}$$

From this and (4.4), the remaining fractions g_V and g_G can be derived:

$$(4.6)\quad \begin{aligned} g_V &= \left(1 + \frac{a_G G_t}{k}\right)^{-k} - \left(\left(1 + \frac{a_V V_t}{k}\right)\left(1 + \frac{a_G G_t}{k}\right) - r\frac{a_V V_t a_G G_t}{k^2}\right)^{-k} \\ g_G &= \left(1 + \frac{a_V V_t}{k}\right)^{-k} - \left(\left(1 + \frac{a_V V_t}{k}\right)\left(1 + \frac{a_G G_t}{k}\right) - r\frac{a_V V_t a_G G_t}{k^2}\right)^{-k} \end{aligned}$$

Between-adult competition

Adult female parasitoids compete over available hosts; we studied both symmetric and asymmetric competition (where one species is competitively inferior, as appears to be the case for *N. giraulti*). Both scenarios were studied using a numerical analysis and individual-based simulations. A parasitoid's competitive ability is a combination of its search efficiency (a_V, a_G) and fecundity (c_V, c_G); a difference in either can cause competitive asymmetry. We only study a difference in fecundity ($c_V > c_G$, which appears to be the case in nature, Grillenberger et al. 2009) and assume both species have the same search efficiency; assuming competitive superiority in search efficiency instead is expected to yield the same results.

Within-host competition

In the above model, c_V or c_G parasitoids emerge from hosts that have been parasitized by only one species. In the case of multiparasitism, the fractions of V and G emerging are given by p_V and p_G, which are functions of the average number of eggs laid per host by both species, E_V and E_G. These can be approximated as follows:

$$(4.7)\qquad E_V = \frac{a_V V_t c_V}{g_V + g_{VG}},\ E_G = \frac{a_G G_t c_G}{g_G + g_{VG}},$$

or the total number of eggs laid per species (the total number of encounters multiplied by the number of eggs laid per encounter), divided by the number of hosts encountered by this species.

The fractions of emerging offspring from multiparasitized hosts, p_V and p_G, are then given by:

(4.8) $$p_V = \frac{E_V}{E_V + E_G},\ p_G = \frac{E_G}{E_V + E_G}.$$

We analyzed the above system of equations numerically, determining whether there is a stable equilibrium where all three species coexist under either symmetric ($c_V = c_G$) or asymmetric competition ($c_V > c_G$).

The above equations make two critical assumptions: first, that the number of offspring emerging from parasitized hosts is always the same, regardless of how many parasitizations occurred. In *Nasonia* species superparasitism is common (Molbo and Parker 1996; Grillenberger et al. 2008; Grillenberger et al. 2009); and while females do avoid overcrowding and lay fewer eggs when superparasitizing (Wylie 1965; Werren 1980), more offspring emerge from superparasitized hosts than from single-parasitized ones (Molbo and Parker 1996). This suggests that hosts have a carrying capacity, but under natural conditions it can exceed the number of eggs laid by a single female.

The second assumption is that the larvae of *V* and *G* are competitively equal. While the relative competitive strengths of the two *Nasonia* species have not been studied, *N. giraulti*'s preference for multiparasitizing (Pérez-Vila et al, in revision) may reflect competitive superiority within the host.

We used individual-based simulations to relax both assumptions and their effects on coexistence; the details are described in the simulation setup below.

Simulation setup

We translated the above system into individual-based simulations for two purposes: to confirm the analytical results, and to study scenarios that are not analytically tractable. We ran 50 replicate simulations for 20,000 generations, after which we recorded for each individual simulation run which parasitoids persisted.

Distribution of encounters

For each host, the number of times it is encountered by both parasitoid species is drawn from a bivariate negative binomial distribution. This distribution is a compound of a bivariate gamma distribution with correlation coefficient r and a Poisson distribution; in biological terms, if $r > 0$ this means the distribution of the parasitoids among patches is correlated, but the parasitoids search randomly within patches, as seems to be the case for *Nasonia* (Grillenberger et al. 2009). We used the method of Minhajuddin et al. (2004) for multivariate gamma sampling to generate bivariate gamma values x_1 and x_2 with correlation coefficient r, which are combined with independent Poisson distributions to draw the final number of encounters with each parasitoid species.

Parasitism and within-host competition

For each encounter, the number of eggs laid by the parasitoid is drawn from a Poisson distribution with average c_V or c_G. After the parasitism phase, the survival rate of the eggs is determined by the total number of eggs ($E_{tot} = E_V + E_G$) and the host carrying capacity ($c_{\max}$). If $E_{tot} < c_{\max}$ all larvae survive into adulthood. If $E_{tot} < c_{\max}$, and both species have equal within-host competitiveness, the survival probability of each larva egg is $p_V = p_G = c_{\max}/E_{tot}$.

Asymmetric within-host competition is implemented by giving G an advantage w_G when multiparasitizing, giving its offspring a higher probability to survive larval competition until emergence, but only when sharing a host with V. In this case, the survival probabilities in multiparasitized hosts are as follows:

$$p_V = \frac{c_{\max}}{E_V + w_G E_G}, \quad p_G = \frac{c_{\max}}{E_V / w_G + E_G}. \tag{4.9}$$

In contrast with the numerical analysis of the equations, where the probabilities p_V and p_G are approximated by the average number of eggs per host, in the simulations these can be calculated exactly based on the actual number of parasitoids that parasitized each host. This can give a more accurate view on how within-host competition plays out, and whether coexistence is possible.

Host and parasitoid reproduction

After parasitism, the number of hosts that escaped parasitism is subject to natural mortality (density dependence). The number that survive after this is multiplied by λ and rounded down, giving the size of the host population in the next generation.

For all parasitized hosts, the number of eggs that develop to adulthood are summed to make up the two parasitoid population sizes in the next generation.

RESULTS

Numerical analysis

For the simplest case, symmetric competition where the two parasitoid species have the same fecundity ($c_V = c_G$), coexistence is possible no matter how strongly correlated the distributions are, as long as the host growth rate λ is high enough to sustain the host population (Figure 4.1a-d).

Next, we looked at the conditions for coexistence under asymmetric competition by introducing a fecundity difference (which seems the case for *N. giraulti* and *N. vitripennis*). When the inferior competitor has a small fecundity disadvantage (c_V = 5.1, c_G = 4.9) the conditions for coexistence are far more restrictive, especially when the distributions are

strongly correlated (Figure 4.1e-h). Increasing the fecundity disadvantage for G (c_V = 5.25, c_G = 4.75) restricts coexistence even further (Figure 4.1i-l). In general, coexistence is favoured by a high host reproductive rate and by strong host aggregation (low k). This last result is consistent with the general finding that strong aggregation of encounters promotes coexistence (Ives 1988a; Klopfer and Ives 1997).

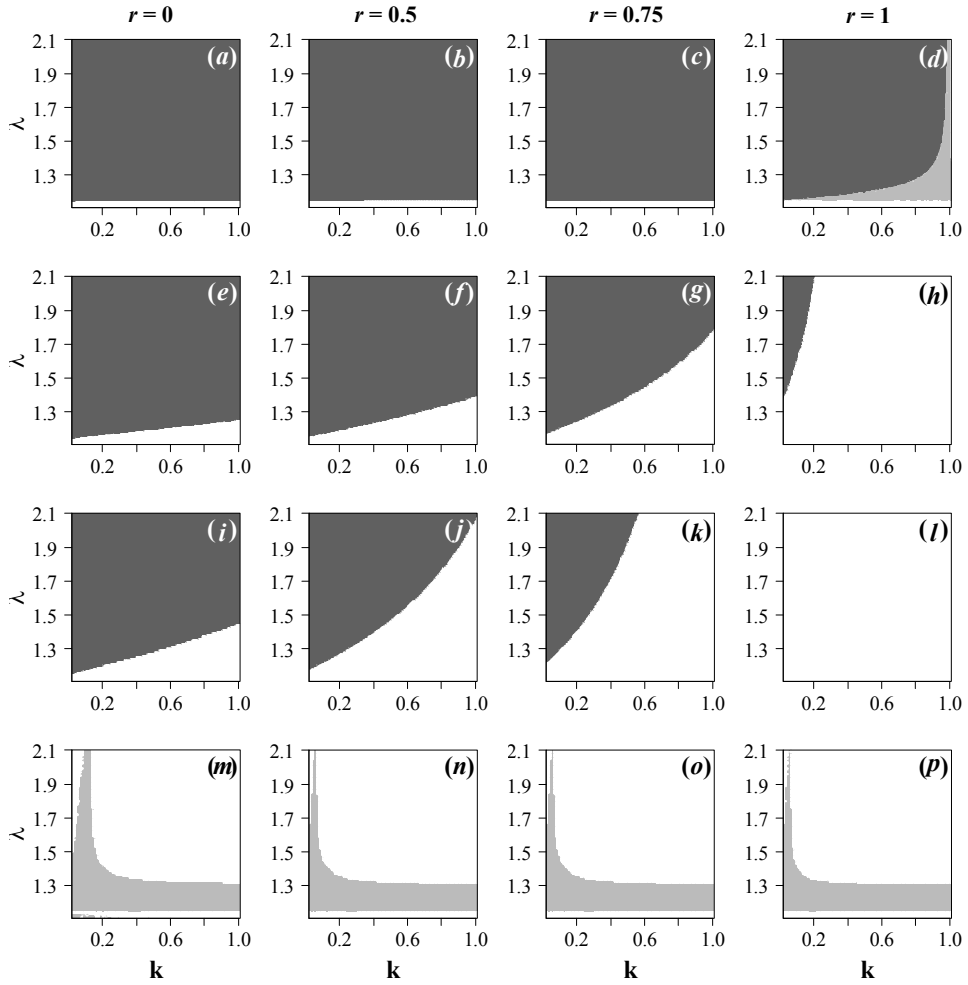

Figure 4.1. Numerical stability analysis of the one-host two-parasitoid system for different values of the correlation coefficient r and the parasitoid fecundities c_V and c_G, plotted against the aggregation parameter k and host growth rate λ. White area: unstable; dark grey: stable; light grey: neutrally stable. In all figures, $a_V = a_G = 3{\cdot}10^{-5}$, $d = 2{\cdot}10^{-5}$. **(a)-(d)** $c_V = c_G = 5$. **(e)-(h)**: small difference in fecundity, $c_V = 5.1$, $c_G = 4.9$. **(i)-(l)**: large fecundity difference, $c_V = 5.25$, $c_G = 4.75$. **(a)-(l)**: $c_{max} = 5$. **(m)-(p)**: no fecundity difference and no within-host competition (all eggs laid emerge as adults), $c_V = c_G = 5$.

Lastly, we looked at the unrealistic scenario of removing within-host competition by modifying the model so all eggs laid by the parasitoids emerge adults:

$$
\begin{aligned}
H_{t+1} &= \lambda H_t \cdot f\left(V_t, G_t\right) \cdot e^{-dH_t} \\
V_{t+1} &= c_V H_t a_V V_t \\
G_{t+1} &= c_G H_t a_G G_t
\end{aligned}
\tag{4.10}
$$

Because there is no competition between larvae within the host, the correlation between the distributions (r) has no effect on the stability of coexistence. More importantly, the two-parasitoid equilibrium is never stable, although there is neutral stability for low host growth rate (Figure 4.1m-p); but even then, long-term coexistence is not expected because stochastic fluctuations in parasitoid abundances are expected to drive one of the parasitoid species extinct. Simulations confirm that there is never stable coexistence of the hosts and both parasitoids in this scenario (see the effect of increasing $c_{\max}$ in the next section).

Simulation results

The simulation results generally confirm the results shown in Figure 4.1 and discussed in the previous section (Figure 4.2a, $c_{\max} = c_V = c_G = 5$). Although coexistence is not possible for all combinations of k and r, as Figure 4.1a-d shows, there is a still wide parameter range for both parameters allowing coexistence of the two parasitoids. Coexistence is promoted by low k (strong aggregation of encounters) and low r (weakly overlapping distributions). When one species is competitively superior, coexistence is still possible but limited to a much narrower range for both k and r (Figure 4.2b), confirming the numerical results shown in Figure 4.1e-l.

Severity of within-host competition

Now we go beyond the results of the numerical analysis, looking at the effect of varying the level of within-host competition by changing the within-host capacity $c_{\max}$. Decreasing within-host competition (increasing $c_{\max}$) makes coexistence less likely; this effect is especially strong if one species (G) has a fecundity disadvantage (Figure 4.3a-d for parasitoids with identical trait values, and Figure 4.3e-h when G has a 10% fecundity disadvantage). The most likely explanation for this is that higher $c_{\max}$ leads to higher parasitoid abundances and lower host abundance, which increases competition between adult parasitoids. In fact, low within-host competition (high $c_{\max}$) can destabilize the system entirely, making coexistence of the host with even one parasitoid species impossible (data not shown). Both of these destabilizing effects are most pronounced when host aggregation is weak (i.e. high values of k).

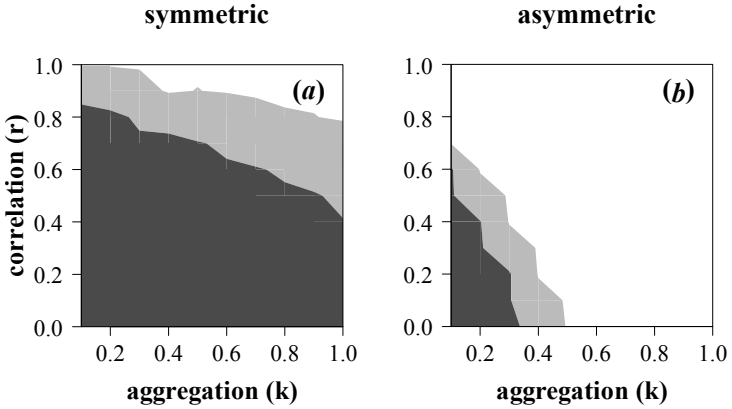

Figure 4.2. Simulation results showing whether the two parasitoids coexist after 20,000 generations, plotted against k and r. Each parameter combination is replicated 50 times. White: never coexistence; dark grey: always coexistence; light grey: sometimes coexistence. **(a)**: $c_{max} = c_V = c_G = 5$; **(b)**: $c_{max} = 5$, $c_V = 5.25$, $c_G = 4.75$. In both figures, $a_V = a_G = 3{\cdot}10^{-5}$, $d = 2{\cdot}10^{-5}$, $\lambda = 1.3$.

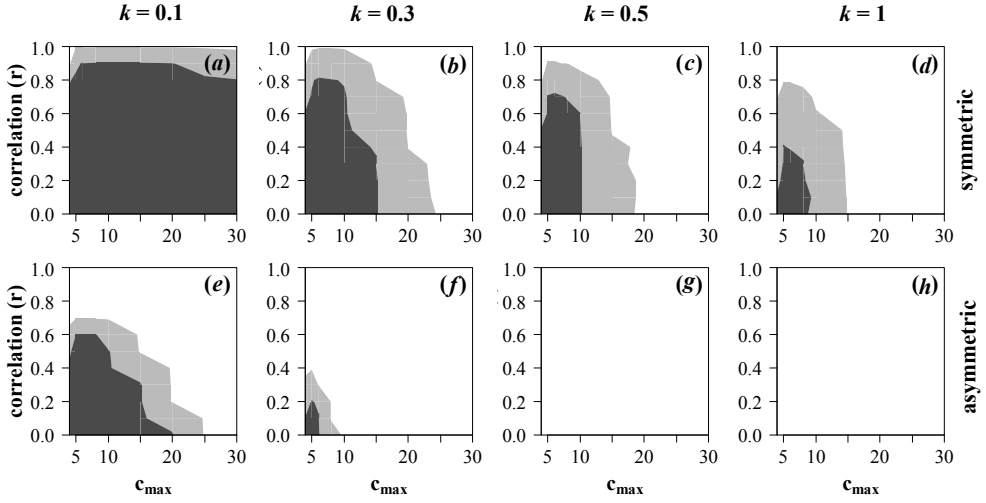

Figure 4.3. Simulation results for different values of c_{max}. **(a)**-**(d)**: $c_V = c_G = 5$, **(e)**-**(h)**: $c_V = 5.25$, $c_G = 4.75$. **(a)**, **(e)**: $k = 0.1$; **(b)**, **(f)**: $k = 0.3$; **(c)**, **(g)**: $k = 0.5$; **(d)**, **(h)**: $k = 1$. In all figures, $a_V = a_G = 3{\cdot}10^{-5}$, $d = 2{\cdot}10^{-5}$, $\lambda = 1.3$. Colours denote the same outcomes as in Figure 4.2.

Within-host advantage

Last, we studied the effect of a within-host competitive advantage (w_G) for *G*, which could compensate for its fecundity disadvantage. Again we chose the fecundities c_V = 5.25, c_G = 4.75, and studied values of w_G from 1.5 - 3.5 and two different values of the within-host carrying capacity c_{max} (6 and 10). We find that a within-host advantage can indeed facilitate coexistence (Figure 4.4), particularly for intermediate values of w_G. If the within-host advantage is too weak, it cannot compensate for the fecundity disadvantage; on the other hand, a very strong advantage makes it possible for *G* to outcompete *V*. This last effect is especially true when the distributions are strongly correlated (high *r*), because a higher correlation means that the two species will share the same hosts more often. This can be seen very clearly in Figure 4.4e, where coexistence is only possible for an intermediate correlation. If it is too low, the two species will not interact enough to make the within-host advantage pay off, but if it is too high, *G*'s advantage can drive *V* extinct.

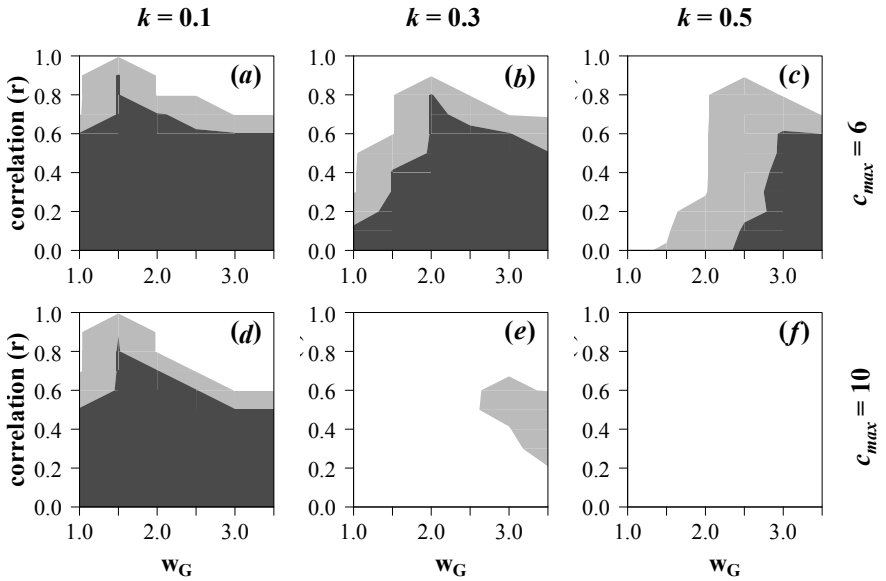

Figure 4.4. Simulation results for different values of w_G. In all figures, c_V = 5.25, c_G = 4.75, a_V = a_G = $3 \cdot 10^{-5}$, d = $2 \cdot 10^{-5}$, λ = 1.3. **(a)-(c)**: c_{max} = 6; **(d)-(f)**: c_{max} = 10. **(a)**, **(d)**: k = 0.1; **(b)**, **(e)**: k = 0.3; **(c)**, **(f)**: k = 0.5. Colours denote the same outcomes as in Figure 4.2.

DISCUSSION

This paper aimed at studying the role of within-host competition on the coexistence of two parasitoid species sharing a host. We find three general patterns: first, coexistence is promoted by weak between-adult interspecific competition (low distribution overlap). Second, the

opposite pattern was found for within-host competition: coexistence is promoted by strong within-host competition. Finally, competitive asymmetry reduces coexistence when the asymmetry is at the adult level; asymmetry in within-host competition, on the other hand, can both promote and reduce coexistence.

Leaving out any other factors first, the results of our numerical analysis are in line with previous studies on the effect of aggregation and correlated distributions (Kakehashi et al. 1984; Klopfer and Ives 1997): coexistence is promoted by a high level of aggregation in the distribution (low k), but reduced by overlap in the parasitoids' distributions; this second effect is especially strong when there is competitive asymmetry between the species. All these results are in agreement with previous models that do not allow for interspecific host sharing (Ives 1988b; Klopfer and Ives 1997).

While the results of our numerical analysis suggest that coexistence of two competitively equal parasitoids is always possible when $r < 1$, and often even when $r = 1$ (complete overlap), the simulation results show that coexistence is more restricted: strongly overlapping distributions ($r \geq 0.8$) never support coexistence, and coexistence is even further limited when the host distribution is not very strongly aggregated (for higher values of k). This discrepancy can be explained by noting that in our equations, the values for the survival probabilities p_V and p_G are only an approximation of the actual fractions. The simulation results are therefore a more accurate reflection of whether coexistence is possible.

In addition to correlation in host encounters and host aggregation, we looked at two more factors that have previously received much less attention: severity and asymmetry of within-host competition. The former gives the counterintuitive result that stronger within-host competition promotes coexistence. Our explanation for this is that increasing the within-host carrying capacity increases parasitoid abundances, which in turn decreases host abundance. This increases interspecific adult competition, making coexistence less feasible. So, while increasing between-adult competition reduces coexistence, increasing within-host competition promotes it.

This latter result also gives an explanation for why interspecific host sharing is very rare in nature. Interspecific host sharing is only possible when the offspring of a single female do not consume the entire host (Miller 1982; Magdaraog et al. 2012; Harvey et al. 2013); in terms of our model, it is only possible when within-host competition is weak (high $c_{\max}$). However, this same condition also severely impairs coexistence. Stable coexistence is unlikely when within-host competition is weak, and more likely when within-host competition is strong. Strong competition leads to strong selection for mechanisms to eliminate heterospecific competitors, which is indeed far more commonly found in nature than interspecific resource sharing.

Second, we found that in case of competitive asymmetry (one species having a lower fecundity) an advantage in within-host competition could compensate for its competitive disadvantage and restore coexistence. However, it is only really effective when within-host competition is severe. If within-host competition is relatively weak, the effect of a within-host advantage is decreased, and hence coexistence is less likely. If two parasitoids can share the same host without overcrowding ($c_{\max} = 10$ in Figure 4.4) coexistence is only possible when

the host distribution is very strongly aggregated. Furthermore, coexistence in all cases is mostly restricted to values of r that are low to moderate, unless there is very strong aggregation (k = 0.1).

Implications for *Nasonia* coexistence

Our model was inspired by the coexistence of two *Nasonia* species competing for the same hosts (blowfly larvae in bird nests), where *N. giraulti* is clearly the inferior competitor and the species' distributions are very strongly correlated; *N. giraulti* is never found in a nest by itself, but only when *N. vitripennis* is also present (Grillenberger et al. 2008).

There are several field data sets available to estimate the values of k. For *N. vitripennis* the two reported values for natural nests are similar ($k \approx 0.72$ for field data on only *N. vitripennis*, Grillenberger et al. 2008,; $k \approx 0.81$ for field data on *N. vitripennis and N. giraulti*, Grillenberger et al. 2009). It is harder to estimate a value for *N. giraulti*, because its abundance in the field is much lower; but Grillenberger et al (2009) gives an estimate of $k \approx 0.1$. If this is correct, this means the encounters of *N. giraulti* are more aggregated than those of *N. vitripennis*. However, it should be noted that these estimates are based on data on emerged offspring, not on the actual distribution of encounters. There may be a discrepancy between these if not all parasitizations are successful, and this will particularly be the case if *N. giraulti* is facilitated by *N. vitripennis*. For this reason, and because the field abundance of *N. giraulti* is much lower, its encounters may only appear to be more aggregated. Because the bivariate negative binomial distribution only has one value for k, it is difficult to estimate the correlation coefficient r with the available data. Using a weighted average of the two values, $k \approx 0.61$, we find an estimate of $r \approx 0.8$. This is consistent with the observation that *N. giraulti* is always found co-occurring in nests with *N. vitripennis* and never by itself, which indicates r must be high to very high.

Our results show that the first of our hypothetical explanations for coexistence, weak within-host competition, does not hold up at all; to the contrary, weak within-host competition reduces the opportunities for coexistence. The second, a within-host advantage, only has a limited effect in promoting coexistence, and mostly for intermediate distribution overlap. Given the strong overlap between *N. vitripennis* and *N. giraulti* in the field, this too seems unlikely to be the explanation for how *N. giraulti* can persist.

Evidently, our model may lack something else of vital importance to understanding coexistence of these two species, so we explored several possibilities. First, we modeled competitive asymmetry by introducing a difference in fecundity, and assumed they have the same search efficiency; we know from field data that *N. giraulti* has a lower fecundity than *N. vitripennis* (Grillenberger et al. 2009; Daoust et al. 2012), but nothing is known about their respective search efficiencies. We tested the robustness of our results with regard to this assumption, and our results indicate that a competitive asymmetry in search efficiency would yield largely the same patterns, though coexistence is more slightly restricted than in our general model (results not shown).

Second, our model assumes that all hosts are equal in terms of quality, and all have the same within-host carrying capacity. In nature, host quality is highly variable, depending on

characteristics such as species, size or developmental stage. Adding variation in quality to our simulations (where each host's individual carrying capacity was drawn from a normal distribution with $\mu = C_{max}$) did affect coexistence depending on the value of C_{max}: for low values, adding variation decreased coexistence, while the opposite was true for higher values of C_{max}. The destabilizing effect of low within-host competition is somewhat smaller when variation in quality is taken into account, but the overall pattern still holds.

Finally, our model makes two critical assumptions: first, that encounters within patches are random; and second, that females always lay the same number of eggs, regardless of whether the host is fresh or already parasitized by either species. Regarding the first assumption, while field data on the distribution of foundresses over hosts showed no evidence for preference for or against hosts used by other females (Grillenberger et al. 2009), laboratory experiments have shown that *N. vitripennis* avoids superparasitism when given the choice between fresh and parasitized hosts (Ivens et al. 2009, S. Pérez-Vila et al, in revision). The same is true for *N. longicornis*, and a host choice experiment with *N. vitripennis* and *N. longicornis* showed they both avoid multiparasitism even stronger than superparasitism (Ivens et al. 2009). The behaviour of *N. giraulti* is very different: it appears to have no aversion to superparasitizing and a preference for multiparasitizing. Taking all of these data together, it appears unlikely that females use hosts within patches indiscriminately, as our model assumes. How nonrandom use of hosts – either through avoiding or through preferring super- / multiparasitism – would affect coexistence is an open question. Avoidance of parasitized hosts would reduce within-host competition (although it would also reduce the number of available hosts, increasing adult competition), potentially lowering the negative effects of sharing a patch. On the other hand, it would lead to a more even distribution of encounters, reducing the level of aggregation (higher k) as well as reducing within-host competition. Both of these effects have been shown in this study to reduce coexistence rather than promote it. Whether either scenario would promote or reduce coexistence requires further study.

The second assumption, that females lay equal numbers of eggs in parasitized and unparasitized hosts, is likely to be more critical. There is ample evidence that *N. vitripennis* adjusts its clutch size to lay fewer eggs when superparasitizing (Wylie 1967; Werren 1980; Werren 1984; Ivens et al. 2009). Similar data is unfortunately unavailable for *N. giraulti*, but consistent with their apparent preference for multiparasitizing: they lay more eggs when multiparasitizing than *N. vitripennis* (Pérez-Vila et al, in revision). A version of the simulations in which both species lay fewer eggs in parasitized hosts, either by conspecifics or heterospecifics, did not yield any results suggesting this alone would improve coexistence. Rather than reducing competition, this scenario leads to lost opportunities for superparasitizing females. The setup of our current model does not allow for females to look for a more suitable host after rejecting an unsuitable one, or to offset the costs of laying fewer eggs in parasitized hosts by laying more eggs in unparasitized ones. A scenario that does allow for either of these two behaviours is definitely more realistic, but is beyond the scope of our current study. A model explicitly allowing avoidance of or preference for parasitized hosts, through either oviposition or clutch size decisions, is a necessary direction for further study.

Our model incorporating within-host competition was inspired by the *Nasonia* system. While the factors we studied seem unsuccessful in explaining coexistence in this particular system, they apply to multiparasitoid-host systems in general. Within-host competition has been a neglected component of multiparasitoid-host models; this is the first model to look at its effects in detail, and we find that it can have a dramatic effect on whether coexistence of two parasitoid species is possible.

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Chapter 5

The evolution and coexistence of divergent parasitization strategies

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ABSTRACT

Superparasitism and multiparasitism refer to a parasitoid laying eggs in a host already parasitized by a conspecific or heterospecific female, respectively. Despite the obvious disadvantage of increasing resource competition for offspring, both behaviours are common in nature. One striking case is multiparasitism between the sibling species *Nasonia vitripennis* and *N. giraulti*: the latter prefers multiparasitizing over parasitizing an empty host. One possible explanation for this seemingly maladaptive behaviour is that *N. giraulti* economizes on its own venom production by taking advantage of venom injected by *N. vitripennis*. We explore the theoretical possibility of the evolution and coexistence of divergent parasitization strategies, using an individual-based simulation model with three evolvable traits: (1) level of venom production, (2) allocation of eggs to unparasitized and parasitized hosts, and (3) allocation of venom to unparasitized and parasitized hosts. Under a wide range of parameter combinations, but only when all three traits evolve simultaneously, we find evolutionary branching into two distinct parasitization strategies: the majority of the population produces a high level of venom, and only parasitizes unparasitized hosts; a minority produces little to no venom and only parasitizes parasitized hosts, taking advantage of the venom injected by the first female. But while evolutionary branching is common, subsequent stable coexistence of the two strategies is restricted to a narrow parameter space. We find that coexistence is promoted by a high cost of venom production and low levels of within-host competition. We discuss our results in the context of microsympatric coexistence in the *Nasonia* system.

INTRODUCTION

Parasitoids are well known to make oviposition decisions based on host characteristics determining its quality, such as species (Haeckermann et al. 2007) or size (Godfray 1986; Hardy et al. 1992; Zaviezo and Mills 2000; Wang et al. 2008), preferentially laying eggs in hosts of high quality to their offspring. One important characteristic determining quality is whether the host has been parasitized before. As resources within the host are limited, laying eggs in a host that has already been parasitized by a conspecific female (superparasitism) or heterospecific female (multiparasitism) yields an obvious disadvantage to offspring fitness. While this is expected to be most severe in solitary parasitoids, where only a single offspring can emerge from a host, it is costly in gregarious parasitoids as well: brood size is negatively correlated with larval survival and body size of emerging adults (Hardy et al. 1992; Vet et al. 1994; Alleyne and Beckage 1997; Rabinovich et al. 2000). Yet despite the ability to discriminate between parasitized and unparasitized hosts being ubiquitous (Dorn and Beckage 2007), superparasitism is common in nature (van Alphen and Visser 1990; Godfray 1994).

Superparasitism is expected to occur when the benefits outweigh the costs; for example, it can be a more efficient strategy when competition over hosts is high and unparasitized hosts are difficult to find, even when the payoff from superparasitized hosts is lower (Parker and Courtney 1984; Visser et al. 1992; Weisser and Houston 1993). In addition, there are various potential advantages to superparasitism that can offset the cost of higher competition. For example, in solitary parasitoids, the second egg can have a higher chance at overcoming the host's immune response (Bakker et al. 1985). In gregarious parasitoids, similar advantages can be found: in *Metaphycus flavus*, superparasitizing increased parasitoid offspring survival by lowering encapsulation rates, and gave a strong advantage to superparasitizing provided the interval between parasitizations was not too long (Tena et al. 2008). Similarly, self-superparasitism was found to be advantageous in *Macrocentrus grandii* because it decreases the probability of total brood failure (White and Andow 2008). Finally, superparasitizing females can benefit from the venom injected by the first female (Dorn and Beckage 2007), potentially allowing them to economize on their own investment in venom production.

Although multiparasitism has been less well studied than superparasitism, numerous examples of it can be found in nature. The same general arguments about the costs of sharing a host with conspecifics apply to heterospecifics, although avoidance of multiparasitism does not always occur even when the cost is high (de Vis et al. 2003; Mahmoud and Lim 2008; Magdaraog et al. 2013). Interspecific host discrimination is rare compared to intraspecific host discrimination, and is mostly limited to recognizing hosts parasitized by closely related species (Wylie 1970; Vet et al. 1984), although some studies have reported a stronger avoidance of multiparasitism than of superparasitism (van Baaren et al. 1994; Ivens et al. 2009). Advantages to multiparasitism have also been observed, albeit rarely: for example, there are several cases in which the multiparasitizing female benefits from viruses or venom injected by the first female, dramatically increasing her offspring's survival when multiparasitizing (Guzo and Stoltz 1985; Cusson et al. 2002). One particularly interesting case is *Nasonia giraulti*, occurring in close

sympatry with its sibling species *N. vitripennis*, which appears to prefer multiparasitizing over parasitizing an unparasitized host (S. Pérez-Vila et al, accepted).

Nasonia are a genus of gregarious parasitoid wasp species, laying several eggs in one host. They parasitize cyclorraphous flies found in bird nests and at carcasses, and are the main parasitoids of species in the *Protocalliphora* genus that parasitize young birds. Individuals mate at emergence on the natal patch (with the exception of *N. giraulti*, which mates almost exclusively within the host), after which females disperse to find suitable hosts (Whiting 1967). Four *Nasonia* species have been described, of which three have a limited geographical distribution: *Nasonia longicornis* in Western North America, and *N. giraulti* and *N. oneida* which occur sympatrically in Eastern North America. They all co-occur with the fourth species, *N. vitripennis*, which has a worldwide distribution (Darling and Werren 1990).

Both *N. longicornis* and *N. giraulti* occur in sympatry with *N. vitripennis*, but their competitive interactions are very different. Multiparasitism in the field between *N. vitripennis* and *N. longicornis* is rare (Grillenberger and Ivens, unpublished data), and a host choice experiment confirmed that both species avoid multiparasitizing more strongly than they avoid superparasitism (Ivens et al. 2009). In contrast, *N. giraulti* is in the field always found co-occurring in nests with *N. vitripennis*, and multiparasitism rates are high (Grillenberger et al. 2009 , Pérez-Vila et al in prep). Even more surprisingly, a host choice experiment has shown that while *N. vitripennis* avoids multiparasitizing (though less strongly than it avoids superparasitizing), *N. giraulti* prefers multiparasitizing over attacking an empty host (Pérez-Vila et al., accepted).

While the effect of host crowding on offspring fitness has not been well studied in *N. giraulti*, in *N. vitripennis* overcrowding leads to smaller offspring (Rivero and West 2005; Sykes et al. 2007), and body size is correlated with longevity as well as fecundity (Flanagan et al. 1998; Rivero and West 2002; Sykes et al. 2007), suggesting host sharing comes at a cost.

With multiparasitism clearly being costly, *N. giraulti*'s seemingly maladaptive parasitism strategy calls for an explanation. It is possible that multiparasitizing confers an advantage large enough to offset the cost. For example, by multiparasitizing, *N. giraulti* might take advantage of venom injected by *N. vitripennis* females, allowing it to economize on its own venom production. While little is definitively known about the levels of venom production and their efficiency and costliness for each species, *N. giraulti*'s closest sibling species *N. oneida* performs poorly when parasitizing on its own compared to when several females are allowed to parasitize simultaneously (S. Pérez-Vila, personal communication), suggesting a lowered ability to successfully parasitize a host by itself. This leaves us with two questions. First, can this difference in parasitization strategies explain coexistence in the field, despite the strong interspecific competition caused by the high multiparasitism rate? And second, given that *N. giraulti* is a sibling species of *N. vitripennis* that possibly evolved sympatrically (Drapeau and Werren 1999; Desjardins et al. 2010), can this be a mechanism through which sympatric speciation can occur?

Existing theoretical models on superparasitism in gregarious parasitoids have generally approached the issue from an optimal foraging viewpoint (Iwasa et al. 1984; Parker and Courtney 1984; Skinner 1985; Strand and Godfray 1989), predicting females should adjust their

clutch size to lay fewer eggs when superparasitizing. However, these models are very simple, not taking into account any other potential effects of superparasitizing on offspring fitness. In this study we develop a more complex model on the evolution of clutch size on unparasitized and parasitized hosts, allowing this to co-evolve with a second trait, venom production, which is assumed to be costly. The most important question we seek to answer is whether we can find evolutionary branching; what conditions promote branching, and whether it leads to stable coexistence of different parasitization strategies.

MODEL

We used an individual-based simulation of host-parasitoid interactions with non-overlapping generations. The ecological host-parasitoid dynamics are based on the Nicholson-Bailey model (Nicholson and Bailey 1935), in which encounters between hosts and parasitoids follow a statistical distribution, typically assumed to be a negative binomial distribution (May 1978). The details of the ecological dynamics are described below under **simulation setup**.

Traits under selection

Each individual has three traits, which together determine its decisions when encountering a host (how much venom to inject and how many eggs to lay), depending on whether or not the host has been parasitized before.

1. Venom production
During parasitism, the parasitoid injects venom to paralyze and kill the host. The production of venom can be assumed to be costly and trade off against another life history trait; here, we assume that venom production is energetically costly and trades off with egg production, so that there is a direct trade-off between fecundity and venom production:

$$c = c_0 - b \cdot v \tag{5.1}$$

Here, c_0 is the maximum fecundity if no energy is spent on venom production; v is the amount or the effectiveness of venom produced; and b is the costliness, or the loss in fecundity per unit of venom produced.

2. Clutch size / host preference
Studying the evolution of clutch size in the context of a possible facilitative effect of superparasitism, our focus is on the evolution of host preference, expressed as relative clutch size. Like previous models (Iwasa et al. 1984; Parker and Courtney 1984; Strand and Godfray 1989), we assume parasitoids do not avoid superparasitizing, but adjust their clutch size

depending on the quality of the host they encounter (parasitized vs. unparasitized). What we study in this model is in which direction they adjust clutch size (laying more eggs in unparasitized or in parasitized hosts) and the strength of this preference.

The average number of eggs a parasitoid lays per encounter is given by her fecundity c, as calculated in eq. (5.1). We assume a direct trade-off between clutch size for unparasitized and clutch size for parasitized hosts: if a female increases her clutch size when encountering an unparasitized host, she will have to lay fewer eggs in parasitized hosts she encounters, and vice versa. This scenario can describe proovigenic parasitoids, which have a fixed number of eggs they can lay in their lifetime, and have to divide them over the hosts they encounter in such a way as to maximize fitness. However, it also includes synovigenic species in which eggs mature at a fixed rate, as long as this rate is slow enough to cause egg limitation (Heimpel and Rosenheim 1998). The clutch size decisions are calculated as described below.

Because the average number of eggs laid over all encounters is assumed constant, the following condition holds:

$$p_U c_U + (1 - p_U) c_P = c \tag{5.2}$$

Here, c_U and c_P are the clutch sizes laid in unparasitized and parasitized hosts, respectively. p_U is the probability, for any encounter between a host and parasitoid, that the host has not been previously parasitized. It can be calculated following the Nicholson-Bailey interaction dynamics, and corresponds to the total number of hosts encountered, divided by the total number of encounters in the population:

$$p_U = \frac{(1 - f(P_t))H_t}{aP_tH_t} = \frac{(1 - f(P_t))}{aP_t} \tag{5.3}$$

Here, H_t and P_t denote host and parasitoid abundance, respectively, and a the parasitoids' search efficiency; aP_t is thus the encounter rate, corresponding to the average number of encounters per host. $f(P_t)$ is the escape function, or the fraction of hosts that avoid parasitism. This fraction is given by the zero term of the negative binomial distribution:

$$f(P_t) = \left(1 + \frac{aP_t}{k}\right)^{-k} \tag{5.4}$$

Here, k is the parameter that describes the degree of aggregation of encounters, with $k = \infty$ corresponding to completely random encounters, and smaller values of k corresponding to stronger aggregation. Some degree of aggregation is generally assumed, caused by nonrandom spatial distribution of the hosts; stable host-parasitoid dynamics are found when $k \leq 1$ (May 1978).

The probability p_U decreases as the superparasitism rate increases; thus it decreases with parasitoid population size P_t and attack rate a, but increases with k. The clutch sizes c_U and c_P for each parasitoid depend on p_U and on its preference trait, here called d_C for "clutch division". They are calculated as follows:

$$c_U = \frac{c \cdot d_C}{p_U d_C + (1 - p_U)(1 - d_C)}$$
$$c_P = \frac{c \cdot (1 - d_C)}{p_U d_C + (1 - p_U)(1 - d_C)} \tag{5.5}$$

d_c takes a value between 0 and 1, where $d_c = 0.5$ corresponds to no preference (laying the same number of eggs in parasitized and unparasitized hosts). $d_c > 0.5$ denotes a preference for unparasitized hosts, and $d_c < 0.5$ a preference for parasitized hosts; $d_c = 0$ and $d_c = 1$ correspond to the extremes of only laying eggs in parasitized and only laying eggs in unparasitized hosts, respectively.

3. Division of venom

Just as a parasitoid can adjust its clutch size based on information about a host's parasitization status, it can likely adjust the amount of venom it injects. The third parasitoid trait, called d_v for "venom division", determines how it chooses to divide the venom it produces over unparasitized and parasitized hosts. Analogous to the host preference trait, this results in two values v_U and v_P determining how much venom an individual injects into unparasitized and parasitized hosts, respectively. They are calculated in the same manner as the clutch sizes:

$$v_U = \frac{v \cdot d_V}{p_U d_V + (1 - p_U)(1 - d_V)}$$
$$v_P = \frac{v \cdot (1 - d_V)}{p_U d_V + (1 - p_U)(1 - d_V)} \tag{5.6}$$

Like the host preference trait d_c described above, d_v takes a value between 0 and 1, with $d_v = 0.5$ corresponding to equal division over unparasitized and parasitized hosts.

Simulation setup

In our simulation the three traits under study, v (venom production), d_c (preference) and d_v (venom division), are each represented as a single continuous allele determining each individual's life history traits as described above. Simulations were run for 50,000 generations; per parameter combination studied, 50 replicate simulation runs were performed.

Each generation consists of three steps: (1) distribution of encounters over the hosts and subsequent parasitism; (2) competition between larvae over resources in the host, determining the number of offspring per parasitoid; and (3) inheritance and mutation.

1. Distribution of encounters and parasitization

At the beginning of each generation, the number of encounters for each host is drawn from a negative binomial distribution with mean aP_t and aggregation level k. After this, per host, for each encounter a parasitoid is drawn randomly from the population. For the first encounter (i.e. when the host is still unparasitized), it lays a number of eggs drawn from a Poisson distribution with $\mu = c_U$ and injects an amount of venom v_U, where c_U and v_U are determined by that individual's inherited traits. If during the first encounter no eggs are laid, the parasitoid injects no venom and the host remains unparasitized for its next encounter. For all subsequent encounters, the same procedure is followed, but using the values of c_P and v_P instead. The total injected venom and number of eggs laid during all encounters determine the larval survival in the host.

2. Larval competition

The survival of larvae into emerging adults is determined by two factors. The total amount of venom injected determines whether the host is successfully paralyzed and killed; if not, no larvae survive. The probability of killing the host is given by a type II functional response:

$$p = \frac{v_T}{v_T + v_0} \tag{5.7}$$

where v_T is the total amount of venom injected by all parasitoids the host encountered, and v_0 is the constant determining the rate of increase. It follows that, if all parasitoids inject venom, superparasitized hosts are more likely to be successfully killed, although the difference may be small.

If paralyzing the host is successful, there is scramble competition among the larvae. We assume the host can sustain a limited number of emerging adults (within-host carrying capacity, $c_{\max}$). The survival probability of each larva is given by

(5.8) $$p = \min\left(1, \frac{c_{\max}}{E_T}\right)$$

3. Reproduction: population dynamics, inheritance and mutation
Each parasitoid produces the number of their offspring that have survived larval competition; again each offspring inherits the traits of its parent with some mutation (see below). The hosts that have escaped parasitism reproduce, according to the Nicholson-Bailey model with density-dependence:

(5.9) $$H_{t+1} = \lambda H_t e^{-mH_t} f\left(P_t\right)$$

where λ is the host intrinsic growth rate and m its mortality due to density-dependence. $f(P_t)$ is the escape function (the fraction of hosts avoiding parasitism), as given in equation (5.4).

As the offspring inherits its parent's traits, mutation occurs with a small probability (0.02). If multiple traits are subjected to evolution, one of the traits is chosen at random per mutation event. The new value for the offspring's trait is drawn from a normal distribution around the old value, with $\sigma = 0.01$.

Parasitoid population size is expected to be an important factor in the evolutionary dynamics, as it affects the superparasitism rate and through this the evolution of both traits. At the same time, population size is affected by these traits as well, creating feedback between ecological and evolutionary dynamics. Moreover, both k and c_{max} affect the level of larval competition directly (k by affecting the rate of superparasitism, c_{max} by affecting the level of within-host competition), as well as indirectly by affecting parasitoid population size. To disentangle these effects, we also studied a version of the model with constant host and parasitoid population sizes. The implementation of parasitoid reproduction in this model and its results can be found in Appendix C.

RESULTS

Evolution of a single trait

Although the three traits are expected to interact with one another, we first studied the evolution of each trait in isolation, keeping the other two traits constant. We analyzed four evolutionary scenarios, each for fixed and dynamic population sizes. In none of these scenarios we observed evolutionary branching in any of the traits. We nevertheless report here the direction of evolution in each scenario, as this will assist in understanding our results for simultaneous evolution of multiple traits.

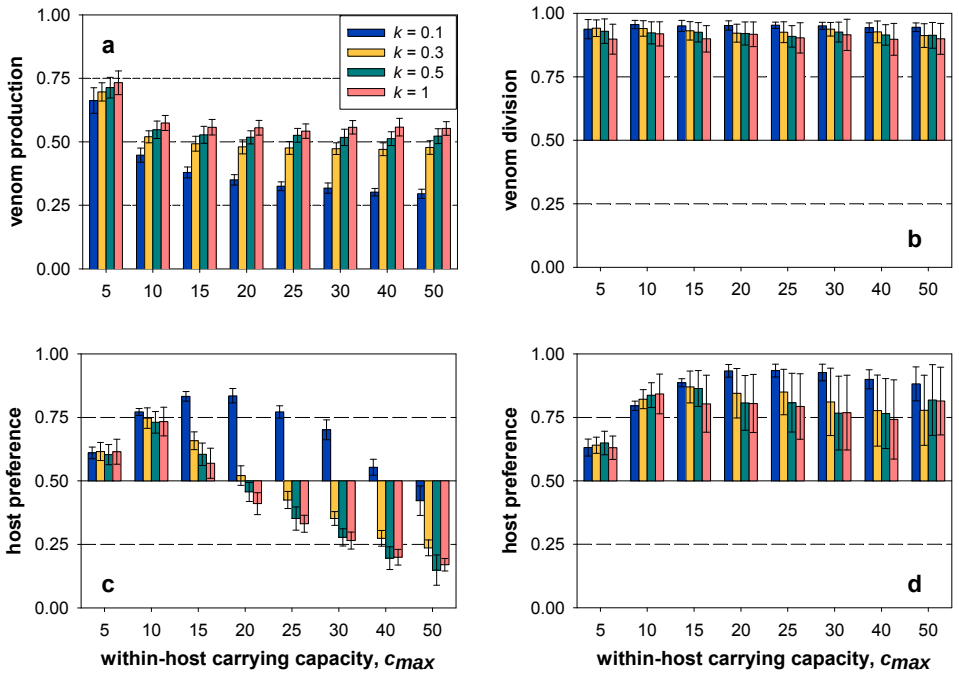

Figure 5.1. Single trait evolution for different values of k and c_{max}, keeping the other two traits constant. (a): evolution of venom production r; $d_c = 0.5$, $d_v = 1.0$, $b = 1.0$. (b): evolution of venom division d_v; $v = 0.5$, $d_c = 0.5$, $b = 0$. (c): evolution of host preference d_c; $v = 0.5$, $d_v = 0.5$, $b = 0$. (d): evolution of host preference d_c; $v = 0.5$, $d_v = 1.0$, $b = 0$. Bars represent mean +/- standard deviation of the population average of the trait under selection, calculated over 50 replicate simulation runs, recorded after 50,000 generations. Other parameters: $a = 3.0 \cdot 10^{-5}$, $c_0 = 5.0$, $v_0 = 0.1$, $\lambda = 1.3$ and $m = 2.0 \cdot 10^{-5}$.

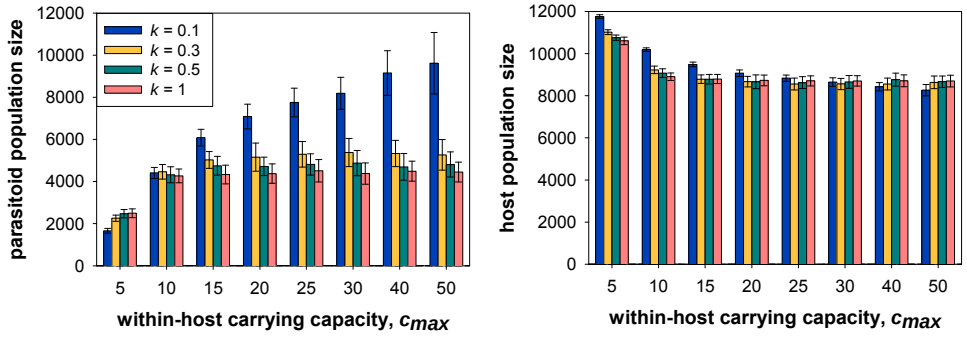

Figure 5.2. Parasitoid and host abundances corresponding to the evolutionary results in Figure 5.1a; all parameters the same as Figure 5.1a.

1. Evolution of venom production

The optimal level of venom production is strongly dependent on the level of within-host competition, and decreases with increasing within-host carrying capacity (Figure 5.1a). Lowered within-host competition increases the probability that any eggs laid will survive into adulthood, and thus selects for higher fecundity. The second factor that affects the evolved level of venom production is the superparasitism rate. Both stronger aggregation of encounters (low k) and a higher parasitoid population size lead to lower venom production (population sizes corresponding to Figure 5.1a are shown in Figure 5.2). As superparasitism is more common, the probability of finding an unparasitized host p_U decreases; when venom is only injected into unparasitized hosts, this means the amount of venom injected per host will increase even if total venom production remains the same. When comparing the actual amounts of venom injected into unparasitized hosts, the effect of superparasitism rate mostly disappears.

As c_{max} increases, the parasitoid population increases in abundance, which causes a decrease in host abundance (Figure 5.2). For $k \geq 0.3$ the average population sizes rapidly level off for $c_{max} \geq 10$; unless encounters are very strongly aggregated, the probability for a host to be found by more than two parasitoids in these cases is very low. Only when encounters are very strongly aggregated ($k = 0.1$) does parasitoid abundance continue to increase with c_{max}. The abundance patterns under evolution of the other two traits are the same.

Although host and parasitoid abundances are expected to affect the course of evolution, all results described in this section were found to hold up in the model with fixed population sizes (Supplementary material, Appendix C, Figure C1). It is therefore the level of within-host competition, not the population sizes, that causes these patterns in evolution.

2. Evolution of venom division

Venom division always evolved in such a way that the vast majority of venom is injected into unparasitized hosts (Figure 5.1b). Both the level of aggregation and the level of within-host competition only have a small effect on the optimal division.

3. Evolution of host preference

We expect that the value that is assumed for the division of venom, d_V, will significantly impact how preference evolves, because the amount of venom injected by superparasitizing females will determine the benefit, if any, to superparasitizing. For this reason we studied two scenarios, $d_V = 0.5$ (equal distribution over unparasitized and parasitized hosts), and $d_V = 1$ (only injecting venom into unparasitized hosts). These two scenarios are the biologically realistic extremes, showing the range in evolutionary outcomes that can theoretically occur.

Equal venom division. In the case where equal amounts of venom are injected regardless of the host's parasitisation status, superparasitizing confers both costs (increased within-host competition) and benefits (multiple doses of venom, giving a higher chance that parasitism is successful). The relative strength of both determines in which direction preference will evolve, so the level of within-host competition is again the most important determining factor in the outcome of evolution (Figure 5.1c). When the within-host carrying capacity c_{max} is small to

intermediate, a preference for unparasitized hosts evolves; the preference is strongest for intermediate values of c_{max}. However, as the severity of within-host competition decreases even further, the relative benefit of superparasitizing increases until it eventually outweighs the costs, leading to selection for a preference for parasitized hosts rather than unparasitized ones. A preference for unparasitized hosts evolves more readily when superparasitism rates are high (low k, high parasitoid population size). The increased level of within-host competition increases the cost of superparasitizing, and a higher carrying capacity is needed to counterbalance this and make superparasitizing pay off.

Venom restricted to unparasitized hosts. If superparasitizing females never inject additional venom, the outcome of evolution changes dramatically (Figure 5.1d). Any benefit of superparasitizing disappears, and consequently, a preference for unparasitized hosts always evolves. As in the previous scenario, the strongest preference evolves for intermediate values of c_{max}. As c_{max} increases further, the impact of within-host competition on larval survival diminishes, resulting in weaker selective pressure for avoiding competition by preferring unparasitized hosts. Moreover, directional selection becomes weak enough for genetic drift to become a prominent force, resulting in large amounts of variation between replicate simulation runs.

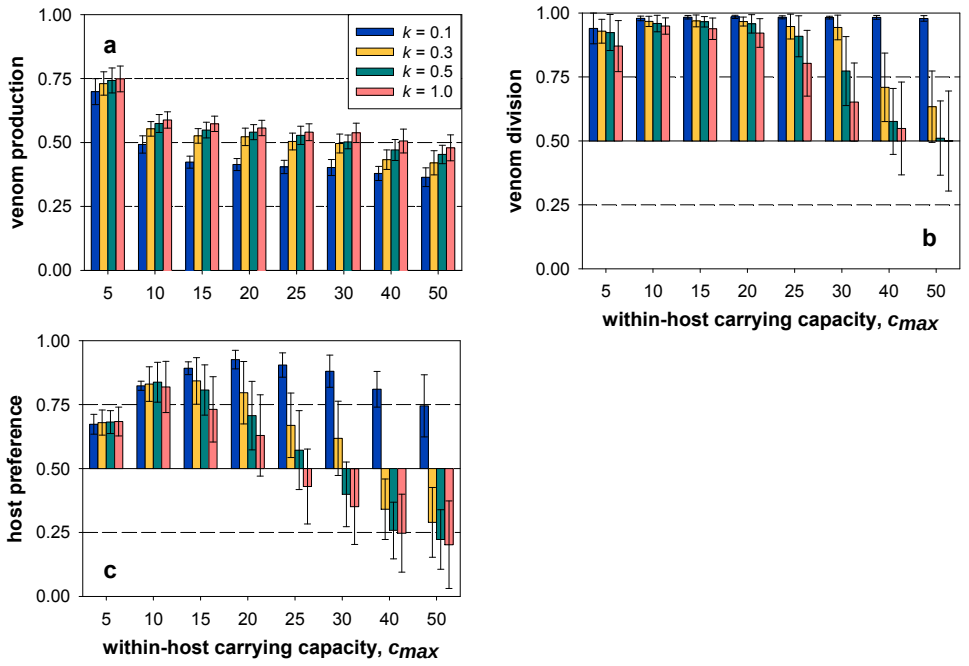

Figure 5.3. Simultaneous evolution of venom production, venom division and host preference. b = 1.0, v_0 = 0.1, a = 3.0·10^{-5}, c_0 = 5.0, λ = 1.3 and m = 2.0·10^{-5}.

Multiple trait evolution

When all three traits are allowed to evolve simultaneously, the results change dramatically, especially for high within-host carrying capacity (Figure 5.3). While venom production shows the same pattern as when it evolves in isolation, the other two traits (venom division and host preference) interact for high values of c_{max}. Venom division always evolved to a value close to 1 when host preference was fixed at $d_C = 0.5$ (Figure 5.1b), but a preference for parasitized hosts causes venom division to become less biased, dropping down to 50/50 (and becoming biased towards injecting in parasitized hosts in many individual simulation runs; see also Figure 5.4). In turn, the more equal division of venom confers an advantage to superparasitizing females, causing a preference for superparasitizing to evolve (Figure 5.3c).

The interaction between these two traits can also be observed between different replicate simulation runs with the same parameter values: there is a positive correlation between the population averages of the two traits, and a wide range of population averages is found for many parameter values (Figure 5.4). In particular, a preference for unparasitized hosts can still evolve even when the expected optimal strategy is a strong preference for parasitized hosts (Figure 5.4b-d), and this appears to be an evolutionarily stable strategy (see also Figure 5.5c). This feedback effect causes the large standard deviations seen for high values of c_{max} in Figure 5.3b-c.

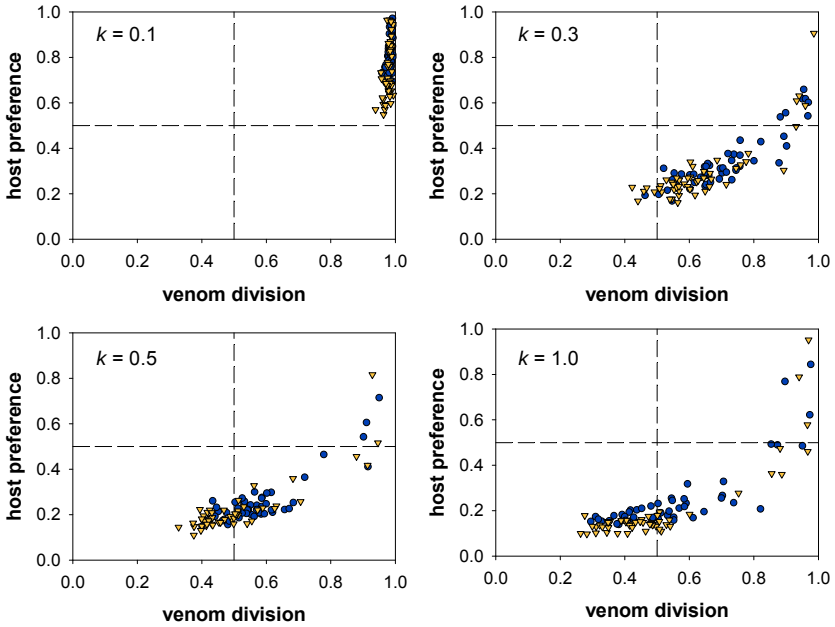

Figure 5.4. Multiple trait evolution results: population averages of the venom division (d_V) and host preference (d_C) traits for different values of k; symbols represent individual simulation runs. Stable coexistence did not occur in any simulation runs. Circles: $c_{max} = 40$; triangles: $c_{max} = 50$. All other parameters the same as in Figure 5.3b.

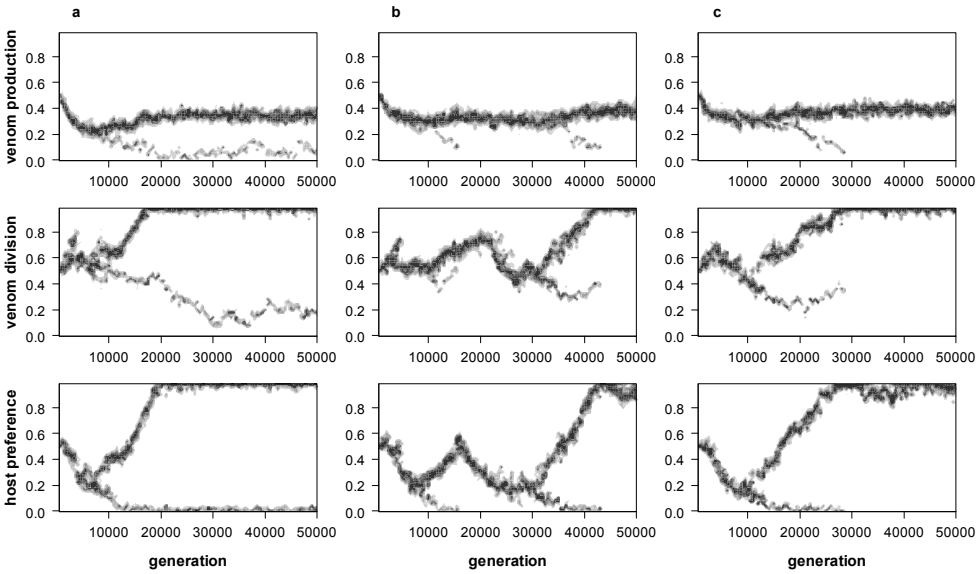

Figure 5.5. Individual simulation runs representative of three different evolutionary outcomes after branching occurs. (a): branching resulting in stable coexistence; (b): cycles of evolutionary branching and extinction of the *P*-strategy; (c): evolutionary branching and extinction of the *P*-strategy, followed by the survival of a single specialized *U*-strategy.

After branching occurs, there are three possible evolutionary scenarios that can follow, the first being stable coexistence of the two strategies (Figure 5.5a). In the other two cases, the *P*-strategy eventually goes extinct (Figure 5.5b-c). What happens next depends on how specialized the *U*-strategy is at the time the *P*-strategy goes extinct. When it is not yet completely specialized on using unparasitized hosts, all three of its traits evolve back to the branching point, and evolutionary branching occurs again (Figure 5.5b). However, if it is completely specialized ($d_V = 1$, $d_C = 1$), it remains specialized, and a monomorphic population of *U*-strategists persists (Figure 5.5c). This last result is consistent with the results shown in Figure 5.4: a monomorphic *U*-strategy, once reached, is an evolutionarily stable strategy.

The probability with which branching occurs, and with which it results in stable coexistence, depends on a number of parameters (Figure 5.6). The most crucial parameter is the within-host carrying capacity: for branching to occur, superparasitizing needs to pay off; low within-host competition (high values of c_{max}) promote branching. The other parameter that strongly affects branching is the costliness of venom production (Figure 5.6b): coexistence increases dramatically as venom production becomes more costly.

The effect of aggregation (k) is less dramatic, but still visible in both branching and coexistence. Very strong aggregation ($k \leq 0.1$) inhibits branching and coexistence, as it results in a very high rate of superparasitism, increasing within-host competition and thereby the cost

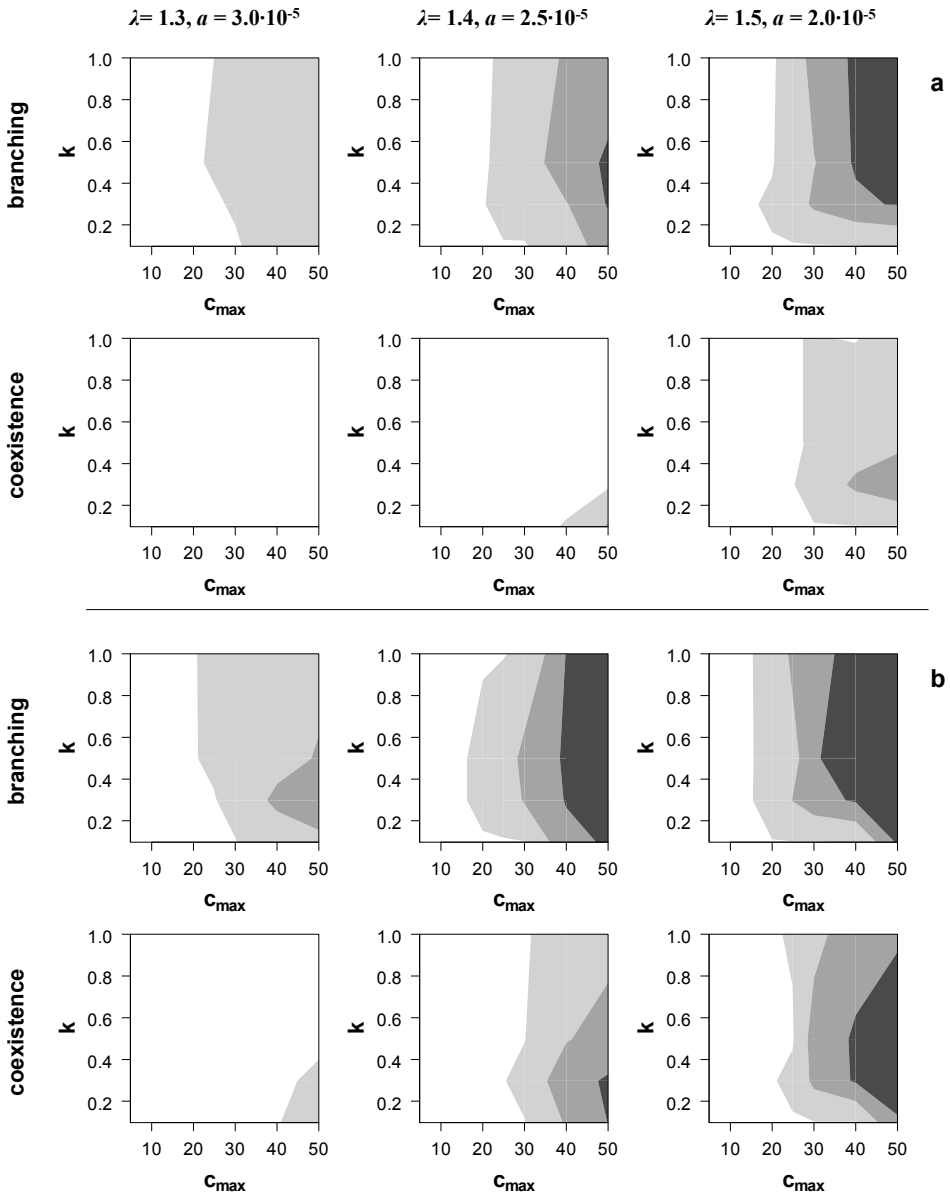

Figure 5.6. The frequency of evolutionary branching and coexistence of two strategies, for three combinations of host growth rate λ and parasitoid attack rate a. (a): low cost, b = 1.0; (b): high cost, b = 2.0. Other parameters: m = 2.0·10^{-5}, c_0 = 5.0, v_0 = 0.1. Colours denote the frequency, scored over 50 replicate simulation runs. White: no branching / coexistence; light grey: 0-50%; middle grey: 50-95%; dark grey: >95%.

of superparasitizing. Conversely, increasing k decreases superparasitism and promotes branching by lowering within-host competition, but impairs coexistence because it leads to lower parasitoid abundance (see Figure 5.2a; branching and coexistence results with fixed population sizes are shown in Appendix C, Figure C3). The highest probability of coexistence thus occurs for intermediate values of k (0.3 – 0.7).

Figure 5.6 also shows the general effect of host and parasitoid population sizes: when host growth rate and parasitoid attack rate have values that sustain higher population sizes, branching and especially coexistence increase dramatically.

DISCUSSION

Existing models on clutch size decisions for gregarious parasitoids take an optimal foraging viewpoint, where the cost of superparasitizing is in time wasted on superparasitizing that could be spent searching for higher quality (unparasitized) hosts (Charnov and Skinner 1984; Parker and Courtney 1984; Skinner 1985; Strand and Godfray 1989); any other costs or benefits to superparasitism are disregarded. Moreover, these models typically focus on host-parasitoid interactions on a single patch, and do not incorporate population dynamics. While there are several models on the evolution of virulence in parasitoids incorporating Nicholson-Bailey population dynamics (Sasaki and Godfray 1999; Tuda and Bonsall 1999), the focus of these models is on the coevolution of parasitoid virulence and host resistance; none of them include superparasitism or within-host competition in their dynamics, and thus do not allow for any potential facilitative effects between parasitoids sharing a host.

In this study we developed a model to study the joint evolution of clutch size decisions and the evolution of virulence, here represented as the level of venom production. For this purpose we adapted a standard Nicholson-Bailey model for host-parasitoid dynamics; our most important modification is the introduction of a within-host carrying capacity. In the standard Nicholson-Bailey model, the number of parasitoid offspring emerging from a host is always the same, regardless of how many parasitoids encountered the host. This is unrealistic in a gregarious species like *Nasonia vitripennis*, in which intraspecific host sharing is common and superparasitized hosts contain larger broods than single-parasitized ones (Molbo and Parker 1996). The introduction of a within-host carrying capacity provides a more realistic model for gregarious parasitoids like *Nasonia*.

In this new framework, our results show that the single most important parameter determining the course of evolution across all scenarios is the within-host carrying capacity c_{max}. This is particularly the case for the evolution of host preference, because this parameter determines the level of within-host competition and thus the cost of superparasitizing. A preference for unparasitized hosts always evolves when within-host competition is the only factor under consideration for larval fitness; this is consistent with results of previous models on clutch size (Parker and Courtney 1984; Skinner 1985; Strand and Godfray 1989) that superparasitizing females should always lay fewer eggs than the first female. But when superparasitizing can confer an advantage in addition to the cost of higher larval competition, a

preference for superparasitizing can evolve, but only if the costs of superparasitizing are sufficiently low.

Although various clutch size models include a within-host carrying capacity (Parker and Courtney 1984; Strand and Godfray 1989), they do not study the effect of this parameter on the relative clutch sizes for the first and subsequent females. Our results indicate that the largest bias towards laying eggs in unparasitized hosts should occur for an intermediate carrying capacity. When the carrying capacity is high, competition is low enough that superparasitizing does not confer substantial costs in larval survival, making it less necessary to discriminate between parasitized and unparasitized hosts. Conversely, when the carrying capacity is low, a strong preference for unparasitized hosts does not pay off either; one possible explanation is that very strong within-host competition makes it less profitable to lay most eggs on a single host.

Our most striking result is that, while evolution of a single trait always leads to a monomorphic equilibrium, the joint evolution of venom production, venom division, and host preference can lead to evolutionary branching into two distinct parasitisation strategies. Again, the within-host carrying capacity is the most crucial parameter in whether branching occurs and whether it can lead to stable coexistence: branching is impossible when within-host competition is too strong for superparasitizing to pay off.

If both strategies persist after evolutionary branching, this eventually always leads to two extreme strategies: one producing venom and only laying eggs in unparasitized hosts (*U*-strategy), and the other producing little or no venom and only superparasitizing, taking advantage of the venom produced by the first female (*P*-strategy). The *P*-strategy always occurs at a lower frequency than the *U*-strategy, which is expected because the *P*-strategy has to rely on hosts previously parasitized by the *U*-strategy. The relative frequencies of the two strategies are determined by the cost of producing venom. When venom production comes at a higher cost, the fecundity of the *U*-strategy decreases, which has two effects: first, fewer eggs are laid by the *U*-strategy in total, so its numbers go down even without within-host competition; and second, it suffers more from competition in superparasitized hosts. Together this makes the *P*-strategy a stronger competitor, increasing its relative abundance in the population.

In principle, stable coexistence of the two strategies is always possible when branching has occurred. In practice, the *P*-strategy often goes extinct stochastically due to its low population size. Stable coexistence is thus most likely when either the frequency of the *P*-strategy in the population is higher (high cost of venom production) or when the total parasitoid abundance is high (high host growth rate; likewise, in the fixed population model coexistence is promoted by high parasitoid abundance (Figure C3)). Similarly, reducing stochastic variation in population dynamics promotes coexistence. In our model the number of eggs laid during an encounter is drawn from a Poisson distribution, and coexistence was more common in a version of the model where the number of eggs laid was strictly equal to the genetically determined clutch size (results not shown).

In the setup of our model, we decided it was reasonable to include a "venom division" trait to our model, despite a lack of empirical evidence that parasitoids inject less venom into parasitized hosts. Removing this trait from the model does not qualitatively change any of the

results. Most importantly, in a two-trait version of the simulation, branching and coexistence both occurred for a wider parameter range than in the three-trait version. The inclusion of the venom division trait allows parasitoids to economize on venom production, by injecting venom only into some of the hosts; without this trait, the costs for the *U*-strategy are higher, resulting in a higher incidence of both branching and stable coexistence (this result is similar to the effect of increasing the costliness of venom). Thus, the inclusion of this third trait constitutes a "worst-case scenario" with regard to evolutionary branching.

One limitation of our model is that it assumes asexual reproduction, directly prohibiting gene flow between the two strategies after branching has occurred. Cross-mating between individuals with different strategies would prohibit branching. Because the coexistence of the two strategies necessitates them sharing a host, this may seem unrealistic. However, theoretical work on sympatric speciation has shown that simultaneous evolution of the ecological traits and assortative mating traits is possible in sexual species (Dieckmann and Doebeli 1999). If assortative mating and reproductive isolation does evolve, this would effectively lead to speciation; the *P*-strategy would consist of high rates of multiparasitism as well as superparasitism, as is seen in the *Nasonia* system.

Implications for *Nasonia* evolution

Our model was inspired by two *Nasonia* species, *Nasonia vitripennis* and *N. giraulti*, that live in close sympatry in Eastern North America, often sharing the same hosts. *N. giraulti* is always found in close association with *N. vitripennis*, never parasitizing a patch by itself (Grillenberger et al. 2009; Daoust et al. 2012); multiparasitism between these two species occurs at a high rate in the field (Grillenberger et al. 2009). Most remarkably, while *N. vitripennis* avoids multiparasitism, *N. giraulti* prefers hosts parasitized by *N. vitripennis* over unparasitized hosts (S. Pérez-Vila et al, accepted).

This study was partly motivated by the question whether this combination of parasitization strategies in *Nasonia* could evolve sympatrically. In terms of our results, *N. vitripennis* is the *U*-strategy while *N. giraulti* is the *P*-strategy. Consistent with our results, *N. giraulti* is far less common in the field than *N. vitripennis* (Grillenberger et al. 2009; Daoust et al. 2012). Our model predicts that the most important parameters determining *N. giraulti*'s abundance, both in absolute numbers and relative to *N. vitripennis*, are the within-host carrying capacity and the costliness of venom production. The carrying capacity in North America is around 25-30 (see Table 1), but data on the costliness of venom is lacking. Such data would allow us to test our predictions on the relative abundances of *N. giraulti* and *N. vitripennis* in the field. Also consistent with our result is the fact that *N. vitripennis* has a holarctic distribution, whereas *N. giraulti* has a very limited geographical distribution, occurring only in a small region in North America. *N. vitripennis*'s strategy is present in all evolutionary outcomes, including those in which the *P*-strategy has gone extinct.

The parasitization strategies of both *Nasonia* species are not as extreme as the strategies that evolve in our simulations. One possible explanation for this is that the two *Nasonia* species are still diverging; it may even be that stable coexistence is not possible for these two species, and

*N. girault*i may go extinct before complete specialization is reached. Alternatively, the extreme strategies found in our simulations could be an artefact of the model setup. Most importantly, our model by necessity assumes that, even after branching, the two strategies are part of one single population. While there is strong overlap in the distributions of *N. vitripennis* and *N. girault*i in the field (the latter is typically found in association with the former, Grillenberger et al. 2009; Daoust et al. 2012), their association is likely weaker than the single-population scenario in our simulations. If their distributions in the field are partly non-overlapping, decreasing the frequency of encounters between individuals with different strategies, the resulting strategies are likely to be less extreme. A two-population model is needed to study the course of evolution under lower degrees of interspecific association, and to study what degree of association is necessary for evolutionary divergence to be feasible at all.

As noted in the previous section, a mechanism for assortative mating is required to prevent gene flow from disrupting the evolved polymorphism. Such a mechanism exists between these two species: while *N. vitripennis* mates after emergence from the host, *N. girault*i mates almost exclusively within the host (Drapeau and Werren 1999; Leonard and Boake 2006), generating assortative mating that appears to be strong enough for *N. girault*i to have abandoned species-specific chemical mate recognition (Buellesbach et al. 2013). This type of mating may have evolved during speciation, effectively reproductively isolating the incipient species.

Not much is known about the mechanisms of speciation in the *Nasonia* complex, and whether it was sympatric or allopatric in origin. It has been speculated that reproductive isolation caused by species-specific *Wolbachia* bacteria may have played a role (Bordenstein et al. 2001), although there is no *Wolbachia*-induced incompatibility between *N. girault*i and *N. oneida*, the two most recenty diverged sibling species that occur in sympatry (Raychoudhury et al. 2010), indicating that cytoplasmic incompatibility is not required for speciation. Likewise, it is unclear why speciation has occurred several times in North America and never in the rest of the world, despite *N. vitripennis* being distributed holarctically; or if evolutionary branching has also taken place elsewhere, why *N. girault*i's parasitization strategy has gone extinct everywhere but in North America. Our results indicate that speciation occurs more readily with a higher within-host carrying capacity. Comparing field data on offspring numbers per host between Europe and North America, there does appear to be a trend for American hosts to have higher carrying capacities, but this difference is not statistically significant (Table 5.1).

Our model provides a plausible mechanism by which speciation may have occurred, although evidence is still only circumstantial. A study on the whole genomes of *Nasonia* species found evidence of rapid directional selection on venom genes between *N. vitripennis* and *N. girault*i (Werren et al. 2010), but this possibly merely reflects the fact that *N. vitripennis* is a generalist using many different host species and *N. girault*i is a specialist on *Protocalliphora* spp., two strategies that require different venom proteins. Furthermore, its closest sibling species *N. oneida* performs poorly on its own compared to when several females are allowed to parasitize simultaneously, suggesting it benefits from superparasitism. While *N. girault*i has a preference for multiparasitizing, it is unclear precisely what benefit it gains from this behaviour. Data comparing the numbers and fitness of *N. vitripennis* and *N. girault*i offspring, either in single

parasitizations or under super- or multiparasitism, would give more insight into the costs and benefits of sharing a host to both species, but is still lacking.

Further empirical studies are needed to determine whether the main predictions of our model hold up: (1) that *N. giraulti* offspring benefit from multiparasitizing (and that *N. vitripennis* offspring do not); (2) that *N. giraulti*'s venom production is lower or that it has a lower potency, having a lowered ability to kill the host or to modify its metabolism to suit the offspring's needs. Answering these questions will bring us closer to understanding the evolutionary origin of *N. giraulti*'s peculiar parasitization behaviour and super- and multiparasitism in general.

Table 5.1 Summary of average offspring per host found in field studies done in Europe and North America.

Reference	**study area**	**host**	**offspring / host**
Grillenberger et al. 2008	Hoge Veluwe / Schlüchtern	Calliphora / Unspecified	14.77 ± 9.94
Molbo and Parker 1996	Sweden	Calliphora, Protocalliphora	25.61 ± 16.91
Peters and Abraham 2010 [a]	Germany	Calliphora	9.3
		Protocalliphora	21.3
		Potemia	9.6
Grillenberger et al. 2009	New York	Unspecified	22.0 (subset of nests)
Daoust et al. 2012	Quebec	Protocalliphora	30.66 ± 20.78 27.83 ± 14.82 *N. v.* 29.64 ± 9.24 20.63 ± 10.01 *N. g.*
S. Pérez-Vila, in prep	New York	Protocalliphora	26.69 ± 13.52
		Average over all	24.71 ± 13.95

[a]No standard deviations were reported in this study

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Chapter 6

Synthesis and Future Directions

Ellen van Velzen

SYNTHESIS

In recent years, interest in the interplay between ecological and evolutionary dynamics has grown dramatically, as it has become increasingly clear that feedbacks between ecological and evolutionary processes can affect biological systems in complex and sometimes unpredictable ways (Fagerstrom et al. 1987; Johnson and Stinchcombe 2007; Kokko and Lopez-Sepulcre 2007; Pelletier et al. 2009; Post and Palkovacs 2009; Schoener 2011). Recent studies on eco-evolutionary dynamics range from the relatively small-scale, such as predator-prey dynamics in simple systems (Yoshida et al. 2003; Yoshida et al. 2007) to complex communities and ecosystem functioning (Harmon et al. 2009; Palkovacs et al. 2009; Seehausen 2009; Bassar et al. 2010). Eco-evolutionary perspectives have been used to study important issues in ecology and evolution, such as evolutionary divergence and speciation (Harmon et al. 2009; Seehausen 2009) and coexistence (Egas et al. 2004; Abrams 2006a; Kremer and Klausmeier 2013), sometimes with contradictory results.

This thesis is centered around two major themes: first, the coexistence of competitors on shared resources or with shared predators; and second, their evolutionary emergence through ecological speciation (evolutionary branching), with a particular emphasis on the joint effects of ecology and evolution. Most recent research into eco-evolutionary dynamics focuses on the effects of rapid evolution (Hairston et al. 2005; Carroll et al. 2007; Hendry et al. 2007; Lankau 2011); in this thesis I used simulations to model evolutionary and ecological processes taking place simultaneously, relaxing the traditional modelling assumption of separate time-scales, but generally still assumed evolution is slower than ecology. Despite this, the results in this thesis show interesting interactions between ecological and evolutionary dynamics.

ECO-EVOLUTIONARY DYNAMICS

For eco-evolutionary feedbacks to occur, two conditions must be met: first, ecological interactions (with competitors, species on other trophic levels, or the environment) must drive evolutionary change; and second, this evolutionary change must affect the original ecological interactions, thus closing the feedback loop (Post and Palkovacs 2009). Both processes have been observed in the models in this thesis.

Ecology affects evolution

This thesis has focused largely on competitive interactions, which have a major effect on evolution in all models considered. I studied the effects of competition in a number of different context: the presence of them at all in a lower trophic level (**Chapter 2**); the symmetry / asymmetry of competition (**Chapter 3**); and the severity of competition and the life stage at which competition plays out (**Chapter 5**). Of course, in addition to competition, evolution is affected by interactions with higher or lower trophic levels, for example the abundance of resources or consumers (**Chapter 2, Chapter 3**).

In a plant-herbivore system with two plants where herbivore preference for each plant evolves, competition between plants can affect herbivore evolution (**Chapter 2**). The most obvious effect is that competition (especially when coupled with asymmetric consumption of the two plants) affects the relative abundances of the two plants; but more importantly, it drives fluctuations in plant abundance, which dramatically changes the fitness landscape for the herbivores, in turn driving the evolution of specialization.

In the context of plant evolution, competition between plants also has a major effect on evolution (**Chapter 3**). Specifically, whether or not the evolution of defense could lead to asymmetric competition (through affecting a plant's competitiveness rather than, or in addition to, its growth rate) determines whether evolutionary branching into different defensive strategies can occur. In addition, in this model a second ecological factor has a major effect on evolution: whether the plant is defending against a generalist or a specialist herbivore. Not only can this affect the level of defense that evolves (investment in defense is often lower against specialist herbivores), but evolutionary branching is only possible when defending against generalist herbivores.

Finally, in host-parasitoid systems, the evolution of host preference is driven mainly by the level of within-host competition among parasitoids (a compound of the level of intraspecific aggregation and the within-host carrying capacity) (**Chapter 5**). Severe within-host competition invariably leads to a preference for unparasitized hosts, but this preference largely disappears as the within-host carrying capacity increases. Most importantly, evolutionary branching is only possible when the within-host carrying capacity is high.

Evolution affects ecology, and eco-evolutionary feedbacks

The converse, evolution affecting ecology, also occurred in the models studied in this thesis: evolutionary change affects plant and herbivore abundances (**Chapter 2, Chapter 3**), generates eco-evolutionary cycles (**Chapter 2, Chapter 3**) and makes coexistence possible in host-parasitoid systems by fundamentally changing the nature of the interaction between competitors (**Chapter 4, Chapter 5**).

The evolution of plant preference in herbivores has several distinct effects on the ecological plant-herbivore dynamics in a two-plant model (**Chapter 2**). Firstly, as herbivores evolve, consumption of the two plant species changes, which in turn affects the relative abundances of the plants. Second, and perhaps more importantly, the level of specialization of the herbivores affects how strongly plants and herbivores interact, which affects population dynamics: specialist herbivores drive larger fluctuations in plant abundance than generalist herbivores. These patterns of abundance (relative abundance and severity of fluctuations) in turn determine the fitness landscape for the herbivores, causing eco-evolutionary feedbacks. This feedback can lead to several different types of evolutionary cycling, as the evolution of a new (often more generalist) herbivore changes the fitness landscape in such a way that at least one herbivore strategy becomes non-viable. For example, as the herbivores evolve into two specialists leading to stronger fluctuations in abundance, the advantage of generalism increases, allowing a more generalist strategy to evolve; the presence of a generalist then dampens the

fluctuations, causing the generalist to lose its selective advantage and go extinct, leaving the two specialists, after which the cycle starts again. This eco-evolutionary cycle is similar to that found by Yamamichi et al. (2011), who modelled the coexistence of a phenotypically plastic generalist with two specialists.

Eco-evolutionary cycling is also found when considering plant evolution (**Chapter 3**). This is what causes the major difference between defending against generalist and specialist herbivores: specialist herbivores are dependent on a single plant species and their abundance is strongly affected by evolution of defense, whereas this is not the case for generalists. Thus, plant evolution can feed back on herbivore abundance; and as herbivore pressure changes, so does selection on defense, causing eco-evolutionary cycles similar to the classic experiment of Yoshida et al. (2003). A second type of eco-evolutionary cycling occurs when disruptive selection causes evolutionary branching: herbivore abundance increases rapidly as less-defended plants evolve, driving these plants extinct and leaving just the well-defended plants, causing herbivore abundance to drop again and defense to evolve back to lower values. Interestingly, this means that eco-evolutionary feedback in this case impairs evolutionary branching and coexistence.

Coexistence is also affected by parasitoid evolution in a host-parasitoid system. Evolutionary divergence in parasitization strategies (preference for unparasitized / parasitized hosts) allows coexistence of two parasitoid species under conditions where this is not possible for non-diverged species (low within-host competition and complete distribution overlap, **Chapter 4**). Given these earlier results on coexistence, it was somewhat surprising to see evolutionary branching in **Chapter 5** under the exact conditions that inhibit coexistence in a purely ecological model. Paradoxically, the two strategies sharing the same hosts is necessary for coexistence, as females following the superparasitizing strategy depend on hosts already parasitized by the other (superparasitism-avoiding) strategy. Intriguingly, this means that evolution changes the interaction between the two competing parasitization strategies from purely competitive to at least partly facilitative. This suggests that not only can evolutionary change affect the strength of ecological interactions, but it can fundamentally change the nature of the interaction altogether. The role of evolution in shaping and changing interactions is an intriguing one, and the possibility of facilitation evolving from competitive interactions especially remains poorly studied (Bronstein 2009), even though facilitation has been implicated as an important driver of biodiversity (McIntire and Fajardo 2014). In **Chapter 5**, facilitation arose as an emergent property in a model consisting only of explicitly modelled competitive interactions, giving one more example of how the outcome of evolution in an eco-evolutionary context can be difficult to predict.

Coexistence: costs and trade-offs

In the context of coexistence between competitors on two resources (e.g. habitats or prey species), the shape of the trade-off in using the two resources has a long history of being used to explain coexistence. The classic model of habitat use by Levins (1962) predicted that a weak (convex) trade-off led to a single generalist strategy, whereas a strong (concave) trade-off led to

coexistence of two specialists. This general result has been confirmed in many models: habitat specialization (Egas et al. 2004), consumer specialization on two resources (Abrams 2006a; Abrams 2006b), or the coexistence of fast-growing opportunist species with strong resource competitors (Kremer and Klausmeier 2013). My results on herbivore specialization (**Chapter 2**) are consistent with these general results: evolutionary branching in plant consumption is only possible for a strong trade-off.

Similarly, several studies have found that a concave trade-off can enable the coexistence of defense strategies, the scenario studied in **Chapter 3**. In a host-parasite model where hosts can evolve resistance against parasites, a convex trade-off between resistance and growth rate always led to a single ESS level of resistance, while a concave trade-off gave rise to evolutionary branching (Bowers and Hodgkinson 2001). In a microbial food web model with a trade-off between defense and growth, Vage et al. (2014) again found coexistence only for a concave trade-off. However, in my model of defense against herbivory in plants, no such relationship between trade-off shape and coexistence was found (**Chapter 3**). A direct trade-off between defense and growth rate, whether linear, convex or concave, always gave rise to a single ESS; to get evolutionary branching or coexistence, a trade-off between defense and a different trait (competitiveness) was required.

This last result is consistent with some previous studies that compare trade-offs between traits, sometimes finding major differences between different trade-off structures. In the evolution of resistance against parasites (Bowers and Hodgkinson 2001), a concave trade-off only leads to evolutionary branching if the trade-off is between resistance and intrinsic growth rate; a trade-off between resistance to parasites and resistance to crowding gave the exact opposite result (convex trade-offs leading to branching, while concave trade-offs gave rise to a single ESS). Similarly, Egas et al (2004), studying habitat specialization using a two-habitat model, found that the probability of coexistence strongly depended on whether the trade-off for using the two habitats affected the intrinsic growth rate or the carrying capacity, with coexistence being much more likely in the latter case.

While the trade-off shape has received a lot of attention from theoretical models, the role of the trade-off structure has been far less well studied; as one striking example, models on plant defense universally use a trade-off between defense and growth rate, while many other trade-offs are possible (Strauss et al. 2002). The results of **Chapter 2** and **Chapter 3** show that while the trade-off shape can be an important explanatory factor in some ecological scenarios, this is not universally the case; and the role of the traits affected by the trade-off deserves far more attention than it has received so far.

FUTURE DIRECTIONS: HERBIVORE AND PLANT EVOLUTION

Although the research in this thesis has given some new insights into eco-evolutionary dynamics in various consumer-resource systems, other questions are still left wide open and some new questions arise. Below, I describe several directions for future research, along with some preliminary results to give some indication of where these directions could lead.

6.1. The speed of evolution vs. ecological dynamics in herbivore specialization

In the context of eco-evolutionary dynamics, the relative speed of ecological and evolutionary dynamics can play a major part in determining the outcome. Several studies have found that slow evolution promotes coexistence of competitors, while fast evolution impairs it (e.g. for specialist-generalist coexistence, Abrams 2006b; coexistence of growth / competition specialists on a fluctuating resource, Kremer and Klausmeier 2013). Moreover, fast evolution of predators and prey can destabilize predator-prey dynamics (Abrams and Matsuda 1997). On the other hand, terHorst et al (2010) found that fast evolution promotes coexistence, while Vasseur et al (2011) found it can either stabilize or destabilize ecological dynamics, depending on the intraspecific and interspecific competition coefficients of the competing species.

Because the speed of evolution can have such large and diverse effects, I looked at the effect of varying the mutation rate on the evolution of herbivore specialization.

Preliminary results

Varying the mutation rate has a strong effect on herbivore evolution, particularly when the plant growth rate r is high (and fluctuations in plant abundance are therefore faster and have a larger amplitude) (Figure 6.1). For both fast-growing and slow-growing plants, increasing the mutation rate leads to more specialization, but the effect is most pronounced for fast-growing plants: when evolution is very slow ($m = 0.001$), a majority of simulation runs give rise to a single generalist, even when the trade-off is strong to very strong ($n > 1.4$). As the mutation rate increases, the other outcomes become more common, with the least generalism found for the highest mutation rate.

Additionally, all types of evolutionary cycling are more common as the mutation rate increases. As the majority of the new evolutionary outcomes found in **Chapter 2** involved evolutionary cycling, this means that, as the speed of evolution becomes very slow relative to the speed of ecological dynamics, herbivore evolution becomes mostly restricted to the original three outcomes again (one generalist, two specialists, or one generalist with two specialists). The exception is the only non-cycling new outcome, one generalist with one specialist, which still occurs even if evolution is slow; but it may still disappear when evolution is slowed down even further.

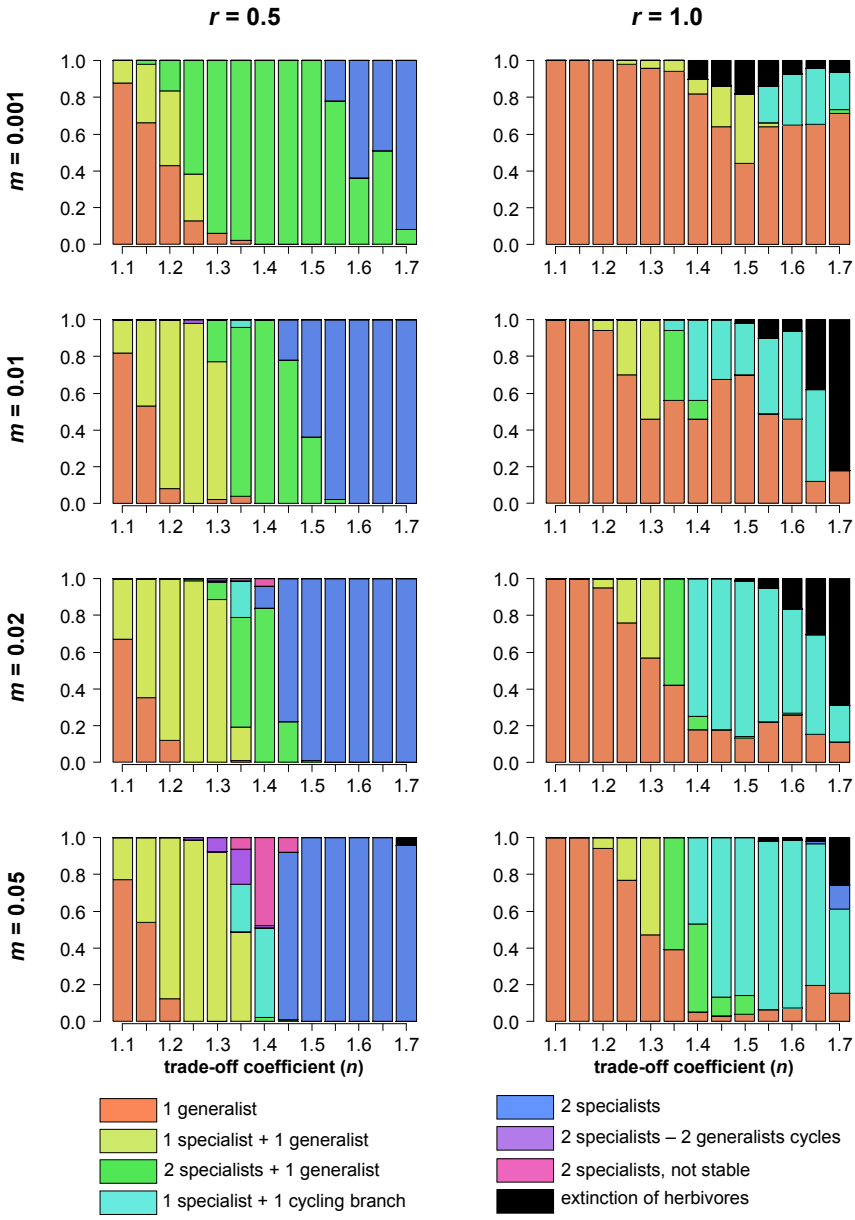

Figure 6.1. Outcomes of herbivore evolution for different mutation rates (m) and plant growth rates (r). Other parameter values: $T = 4.5 \cdot 10^6$, $c_P = 1.0$, $c_H = 2.0$, $a = 10^{-5}$, $t_h = 0.1$, $e = 0.25$, $d_P = 0.05$, $d_H = 0.4$; mutation step size = 0.01. Colours denote evolutionary outcomes, recorded after 100,000 time steps; each bar represents 50 simulation runs, except in the case of $m = 0.05$, where each bar represents 100 simulation runs.

In general, it appears that varying the speed of evolution can have a major impact on which types of herbivores can evolve, and whether evolution results in stable coexistence or branching / extinction cycles. However, these preliminary results raise new questions. While they certainly suggest that the speed of evolution can play a major role, the range of mutation rates studied is still very limited, leaving out both very slow and very fast evolution. Particularly the latter has been implicated in dramatically altering eco-evolutionary dynamics (Yoshida et al. 2003; Yoshida et al. 2007; Schoener 2011; Yamamichi et al. 2011); theoretical studies have predicted that it can either impair coexistence or promote it (Abrams 2006b; terHorst et al. 2010; Vasseur et al. 2011; Kremer and Klausmeier 2013). The preliminary results described here suggest that fast evolution leads more easily to branching / extinction cycles and, thus, to less stable coexistence in the long run.

A related factor I have not studied at all is the effect of varying the mutational step size. In all simulations I have used only mutations with small effect (drawing the new trait value from a normal distribution with $\sigma = 0.01$), allowing only gradual evolution. Allowing larger mutations can have a significant effect on evolutionary dynamics, particularly whether or not branching can take place (Ito and Dieckmann 2012; Sagitov et al. 2013); this may yet again change the outcome of herbivore evolution. Similar effects may be found by including immigration: if herbivores with a radically different strategy from those present in the population invades, it may allow coexistence of combinations of strategies that cannot be reached through gradual evolution (see e.g. Kisdi 2002; Egas et al. 2004). How all of these factors together may shape the eco-evolutionary dynamics is difficult to predict, and this is certainly a worthwhile avenue for further investigation.

6.2. Evolution of herbivore specialization on three plant species

Traditionally, models of specialization and generalist-specialist coexistence use a consumer-resource structure with two resources (Egas et al. 2004; Abrams 2006a; Abrams 2006b). While such simple models can give a lot of insight into fundamental questions – e.g. under what conditions generalists and specialists can evolve or coexist – their use is limited due to the very limited number of possible strategies that can be supported by two resources. Recent work has shown that more complex outcomes are possible when more realism or complexity is added to these models (e.g. behavioural responses, Rueffler et al. 2007; competition between resources, this thesis, **Chapter 2**), but one extension that has, to my knowledge, not been studied is extending the model to more than two resources. The range of possible evolutionary scenarios and combinations of herbivore strategies increases exponentially as the number of resources increases, but which of these are possible, evolutionarily attainable or evolutionarily stable is an open question.

To study just one possible scenario, I simulated the evolution of herbivore preference on three plant species, modifying the simulation used in **Chapter 2**.

Preliminary results

Simulating herbivore preference in a three-plant system for only a limited parameter range for plant growth rate r and a single value for total nutrients T (intermediate, $T = 4.5 \cdot 10^6$) results in a large diversity of different evolutionary outcomes (Figures 6.2, 6.3). Most of the general patterns found in the two-plant model are upheld here: the level of specialization depends on the severity of the trade-off (cost for generalism, n) and on plant intrinsic growth rate (r), with most specialization found for high n (strong trade-off) and low r (slow-growing plants). Extinction of herbivores is more common here than in the two-plant model, but again occurs mostly when the trade-off is strong to very strong (high n).

Apart from the extreme evolutionary outcomes (1 generalist and 3 specialists), eight in-between patterns of specialization are found. All of these include at least one herbivore that is partly-specialized, consuming 2 out of the 3 plant species available. Three evolutionary outcomes include only these herbivores ("2/3 generalists", Figure 6.2, outcome 2-4); in two

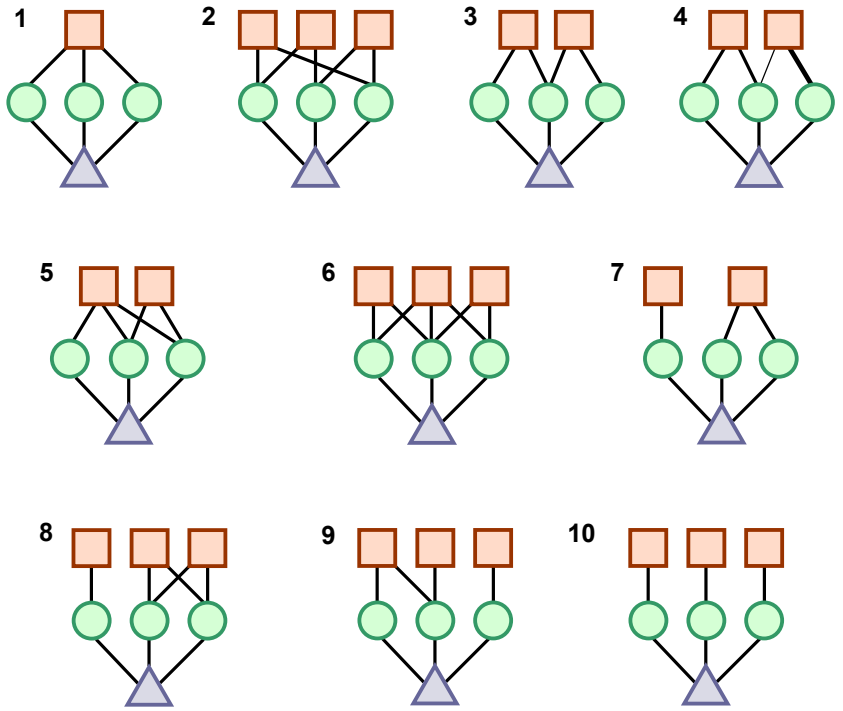

Figure 6.2. Patterns of specialization found in the three-species simulations. Herbivores are represented by squares, plants by circles, and nutrients by triangles. (1) 1 generalist. (2) 3 2/3 generalists (each consuming 2 of the 3 plant species). (3) 2 2/3 generalists. (4) 2 2/3 generalists, where one has a strong preference for a single plant species. (5) 1 generalist and 1 2/3 generalist. (6) 1 generalist and 2 2/3 generalists. (7) 1 specialist and 1 2/3 generalist. (8) 1 specialist and 2 2/3 generalists. (9) 2 specialists and 1 2/3 generalist. (10) 3 specialists.

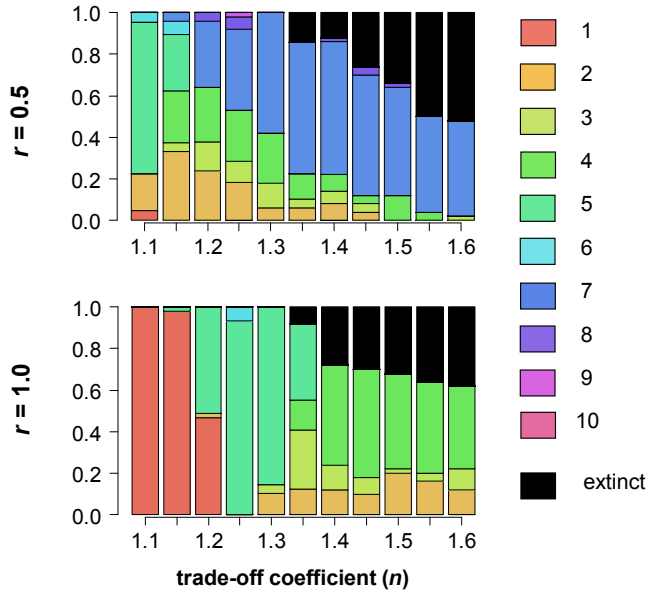

Figure 6.3. Herbivore specialization on 3 plants. Colours denote different evolutionary outcomes; numbers in the legend refer to the outcomes shown in Figure 6.2. Each bar represents 50 simulation runs, recorded after 100,000 time steps. Other parameters: $T = 4.5 \cdot 10^6$, $c_P = 1.0$, $c_H = 2.0$, $a = 10^{-5}$, $t_h = 0.1$, $e = 0.25$, $d_P = 0.05$, $d_H = 0.4$; mutation step size = 0.01; mutation rate = 0.02.

outcomes, they coexist with a generalist consuming all three plant species (Figure 6.2, outcome 5-6); and in the last three, they coexist with at least 1 complete specialist consuming only one plant species (Figure 6.2, outcome 7-9). While many other combinations of generalists and specialists are imaginable, these are the only outcomes found in these simulations. I never found more than three herbivores coexisting on the three plant species, i.e. the number of herbivore strategies did not exceed the number of plants available, while this is not only possible but common in the two-plant model (Abrams 2006a, this thesis, **Chapter 2**).

The most striking result, especially when comparing these results to those of the two-plant model, is that no branching / extinction cycles or other types of evolutionary cycling occurred at all. While the mutation rate used in these simulations was relatively low ($m = 0.02$; see the results of section 6.1 above), the same parameter values did generate evolutionary cycling in the two-plant model (see Figure 6.1).

This extended model with three plant species is clearly still a strongly simplified model, and does not itself give much insight into evolution in more realistic communities+ but it raises some intriguing possibilities and questions. Some of the patterns found in this pilot study strongly resemble those of the two-plant model (e.g. specialization increasing with a stronger trade-off), while others (particularly the lack of evolutionary cycling) are very different. I did not exhaustively explore all parameter ranges to determine whether evolutionary cycling can be found under other conditions, but these results suggest the interesting possibility that

evolutionary cycling could be limited to the two-plant scenario only; although why this should be the case is unclear, and opens an interesting avenue for further study.

The same applies to the result that the number of herbivores coexisting can never exceed the number of plants: while it is unclear whether other parameter ranges could support more than three herbivore strategies, the fact that this did not occur even once in the parameter range I did explore is suggestive. If these major conclusions drawn from classic two-resource (in this case, two-plant) models really hinge on the two-resource assumption and do not hold up if this assumption is relaxed, we should be careful about drawing general conclusions from this type of simple model. But for which conclusions this is the case, and what would happen if the model is extended to even more plant species, is currently still an open question.

6.3. Plant-herbivore coevolution

Although the evolution of consumer specialization on two resources has been studied extensively (Egas et al. 2004; Abrams 2006a; Abrams 2006b; Rueffler et al. 2007, this thesis, **Chapter 2**), and the same is true for the evolution of vulnerability to predation in prey sharing a predator (Abrams 2000; Abrams and Chen 2002; Abrams and Chen 2002), to our knowledge the effect of co-evolution between consumers preference and defense in resources has not been investigated. Some simpler models on plant-herbivore systems have shown that plant-herbivore co-evolution may have far more complex results than evolution in plants or herbivores alone. For example, Loeuille and Loreau (2004) found that evolution in a single trophic level had straightforward eco-evolutionary effects, with two potential different outcomes at most; but when co-evolution was allowed, the number of possible outcomes in one model increased to 32. Because plant and herbivore evolution may interact in complex and unpredictable ways, this may be the single most important and interesting avenue for further research.

To get some idea of how plant-herbivore co-evolution would play out in this system, I combined the herbivore specialization model of **Chapter 2** and the plant evolution model of **Chapter 3**, assuming a direct cost for evolution of defense in plants (decreasing growth rate). Herbivore evolution was simulated using the lineage-based simulation of **Chapter 2**, while plant evolution was added to this model in a fairly simple way. Each time step, one plant species was chosen at random and allowed to "mutate": a new value for its investment into defense was drawn from a normal distribution around the current (resident) value, with a very small standard deviation ($\sigma = 0.001$). Its fitness and that of the resident were calculated as their net growth rate in the current herbivore population, and the strategy with the higher fitness was set as the new resident strategy. Because evolution is modelled in very different ways on the plant and herbivore level, it is difficult to compare the rates of evolution on the two trophic levels, but with the parameters used, they appear to be on the same timescale (see Figure 6.6).

Because I am here mostly interested in whether different herbivore strategies evolve under plant-herbivore coevolution, I chose a parameter range that includes all eight possible herbivore outcomes of **Chapter 2** ($T = 4.5 \cdot 10^6$; $r = 0.5 - 1.0$).

Preliminary results

Effects on herbivore evolution

The evolution of plant defense has a significant effect on herbivore evolution, especially for high plant intrinsic growth rate (Figure 6.4). The most noticeable result is that pure generalism almost entirely disappears, even for a relatively weak trade-off. The reason for this is that some level of defense always evolves against a single generalist herbivore, regardless of how plant and herbivore evolution proceed afterwards (see Figure 6.6). This has two effects: first, it decreases the plant growth rate (because defense is costly), dampening the fluctuations in plant abundance and decreasing the advantageous effect of generalism. Second, it decreases the quality of plants, increasing the advantage of specializing. These two effects together give enough of a disadvantage to generalists that some level of specialization almost always evolves for the parameter range studied (though not when the trade-off is convex ($n < 1$, results not shown)).

The second major effect is that plant evolution appears to stabilize the evolutionary dynamics of the herbivores, leading to less evolutionary cycling; one of the types of cycling (2 generalists – 2 specialists) disappears entirely, reducing the number of possible evolutionary outcomes. I found no new evolutionary patterns in any of the simulations.

For all growth rates, a lower cost of defense generally leads to a higher level of defense (Figure 6.5), subsequently leading to more specialization, though the difference in herbivore evolution is relatively small, especially for higher intrinsic growth rate (Figure 6.4, 6.5). It appears that including plant evolution at all is what causes the major differences in herbivore evolution, while the level of defense that evolves plays a much smaller role.

Plant evolution and plant-herbivore coevolution

Looking at the results of plant evolution in response to herbivores, several patterns are immediately apparent. Most importantly, while the type of cost of defense used in this model (direct cost, lower growth rate) never leads to coexistence of different defense strategies when defending against a single type of herbivore (either generalist or specialist), evolutionary divergence can happen when defense co-evolves with herbivore specialization (Figure 6.5, 6.6). The initial evolutionary response of the two plants, before the herbivores have evolved a significant degree of specialization, is always the same (Figure 6.6); but subsequent herbivore evolution in turn affects plant evolution in such a way that coexistence of different strategies is possible. In fact, coexistence of an undefended and a well-defended plant is overall the most common outcome of plant evolution (Figure 6.5).

The feedback between herbivore and plant evolution is apparent in several ways. The severity of the trade-off for the herbivore is a major determining factor in how plant defense evolves, with higher levels of defense for weaker trade-offs (Figure 6.5). This appears mostly a factor of the types of herbivores that evolve for a given trade-off. In general, defense always evolves to nonzero values except in the case of complete herbivore specialization, in which case a no-defense strategy for both plants is common (Figure 6.5; see Figure 6.6f). Conversely, the

highest levels of defense evolve against generalists (the few simulation runs in which herbivores evolve into a single generalist, both plants evolve high defense, and high + medium defense is associated exclusively with 1 specialist + 1 generalist herbivore).

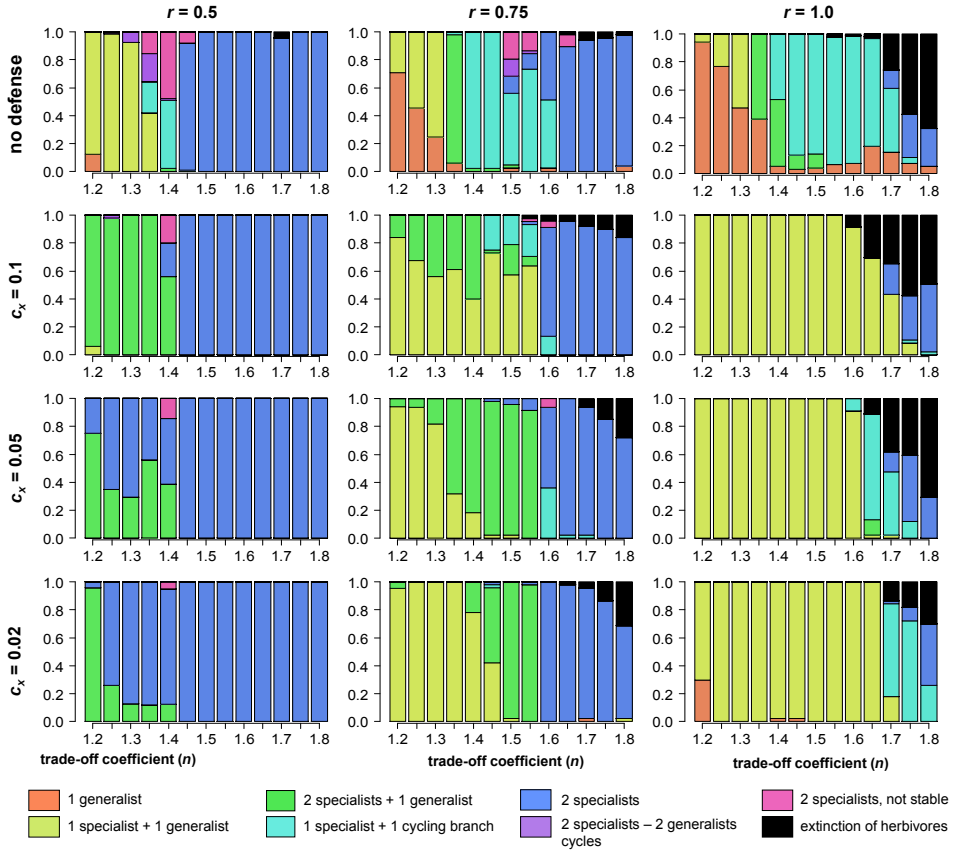

Figure 6.4. Herbivore outcomes for only herbivore evolution (top row) and plant-herbivore coevolution (bottom 3 rows). In all, $T = 4.5 \cdot 10^6$, $c_P = 1.0$, $c_H = 2.0$, $a = 10^{-5}$, $t_h = 0.1$, $e = 0.25$, $d_P = 0.05$, $d_H = 0.4$. Herbivore mutation step size = 0.01, mutation rate = 0.02; plant mutation step size = 0.001; number of time steps = 200,000. Efficiency of defense (e_x) = 1.0.

To give a more detailed look at plant-herbivore coevolution, Figure 6.6 shows the results of individual simulation runs for part of the parameter range ($r = 0.75$, $1.4 \leq n \leq 1.6$). There is a clear interaction between the evolutionary outcomes for herbivores and plants, but also between these and the herbivore trade-off strength n. For example, for lower values of n, the 2-specialist 1-generalist is associated with a combination of high / low defense; whereas for a stronger trade-off ($n = 1.5$), this combination of herbivore strategies is always associated with two weakly-defended plants (Figure 6.6c, 6.6d).

Whether herbivore evolution mostly drives plant evolution or vice versa is difficult to determine with just these results. As an example, in the case of 1 generalist + 1 specialist

herbivore, the two plants suffer different levels of herbivory, leading to divergence in their investment into defense. However, the interaction can go either way. First, the plant suffering more from herbivory can evolve higher defense, as would be expected from models on plant defense (Fagerstrom et al. 1987; Ito and Sakai 2009; Krzysztof Janczur 2009). On the other hand, if one plant evolves a higher level of defense, it makes sense for herbivores to avoid that plant. The well-defended plant can be either the most-consumed or the least-consumed one, depending on the way this interaction goes; and both of these patterns are indeed found (compare Figure 6.6a to 6.6b).

While these results already suggest some interesting interactions between plant evolution, herbivore evolution and their ecological dynamics, it barely scratches the surface of the subject. The parameter range studied is very narrow; in addition, I assumed a direct trade-off for plant defense, while a different trade-off may lead to very different results (see **Chapter 3**). Ideally, plant evolution would be simulated in the same way that herbivore evolution is (i.e. starting with a single plant and allowing evolutionary branching and/or extinction), potentially allowing complex plant-herbivore communities with any number of species to evolve from a single plant and herbivore. Evolution of herbivore preference may strongly depend on the number of plant species present (see section 6.2), increasing the potential complexity of eco-evolutionary feedbacks in such a model.

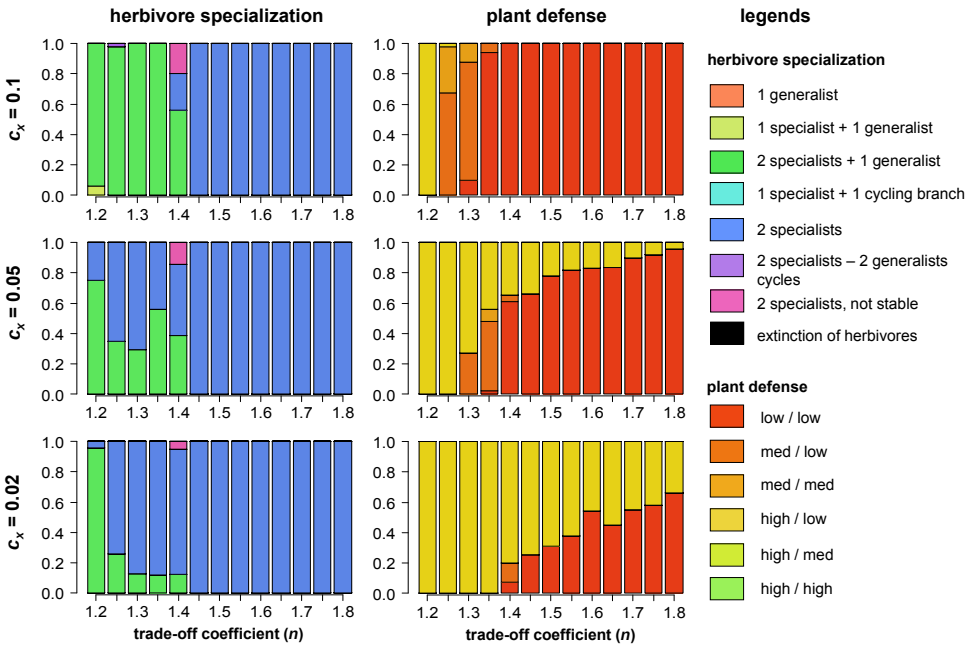

Figure 6.5 Evolution of herbivore specialization (left) and plant defense (right) for $r = 0.5$; all other parameters the same as in Figure 6.4. Level of defense for both plants was recorded at the end of each simulation run and categorized into low / no defense (defense < 0.1), medium ($0.1 \leq$ defense ≤ 0.4) and high (defense > 0.4).

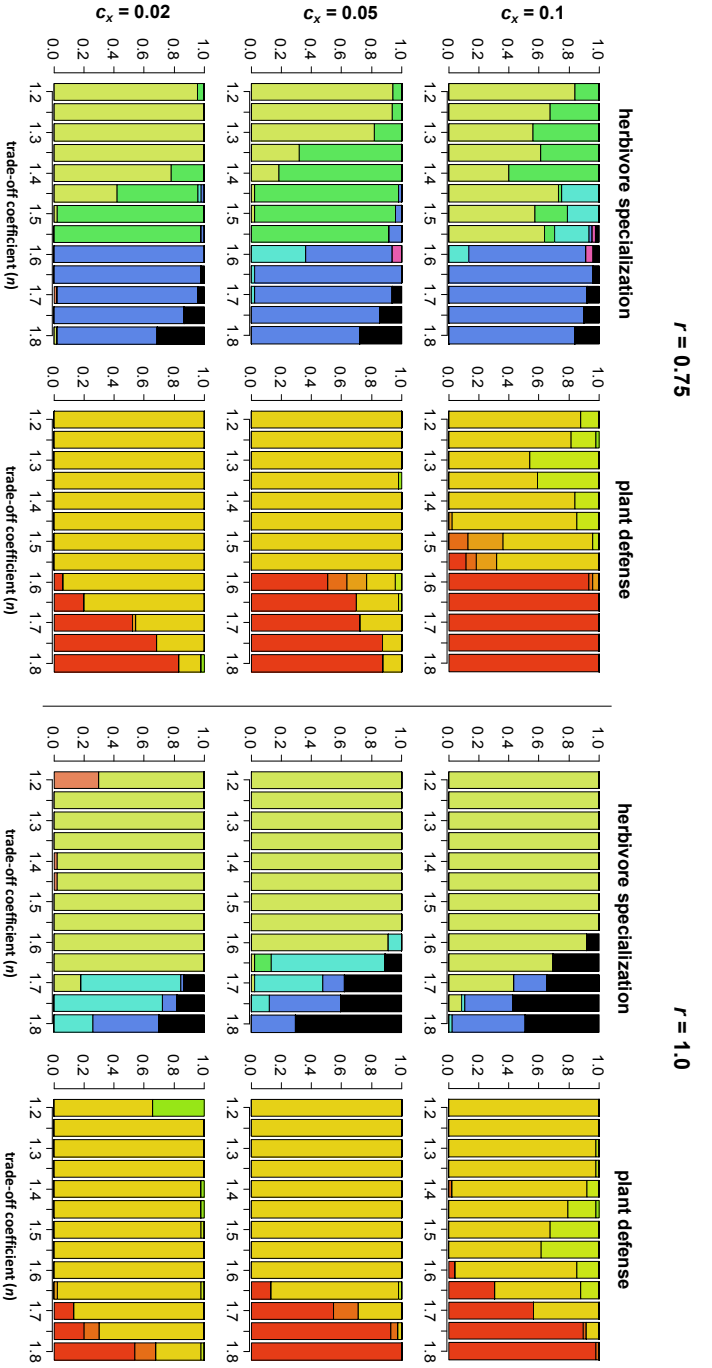

Figure 6.5 (cont.) Evolution of herbivore specialization and plant defense for $r = 0.75$ and $r = 1$.

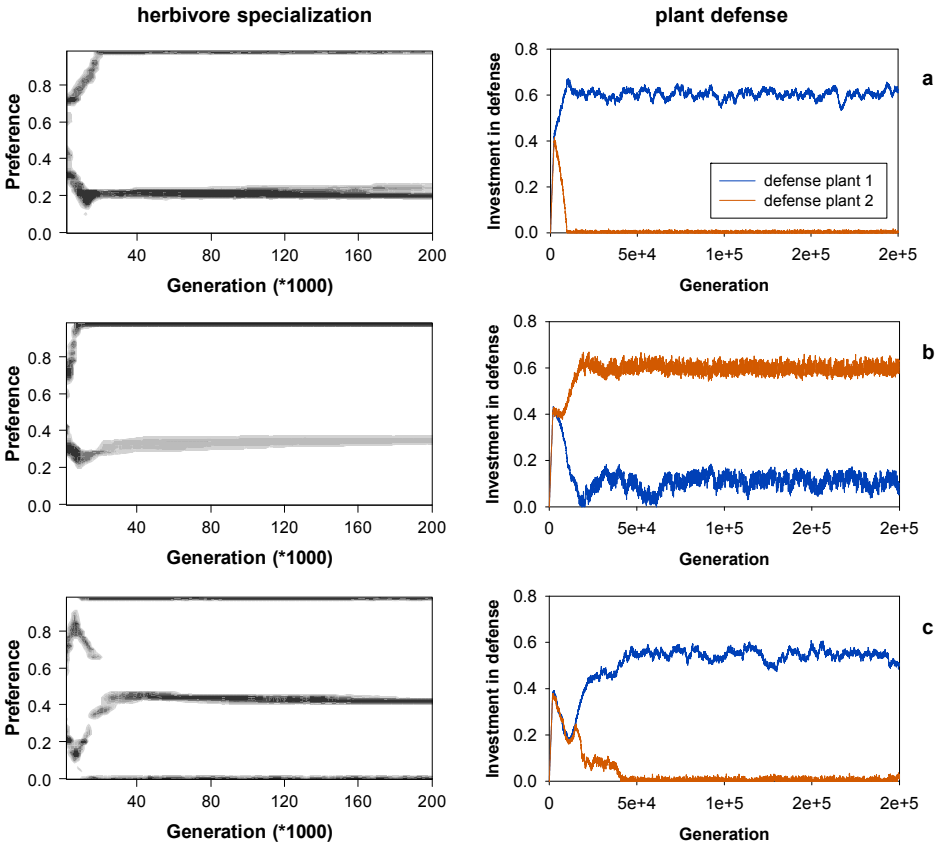

Figure 6.6. Examples of individual simulation runs showing the different co-evolutionary scenarios found for the parameters $r = 0.75$, $\varepsilon_x = 0.1$, $1.4 \leq n \leq 1.6$. (**a**) $n = 1.4$: 1 generalist + 1 specialist; 1 well-defended and 1 undefended plant, with the most attacked plant evolving high defense. (**b**) $n = 1.4$: 1 generalist + 1 specialist; 1 well-defended and 1 poorly-defended plant, with the least attacked plant evolving high defense. (**c**) $n = 1.4$: 1 generalist + 2 specialists; 1 well-defended and 1 undefended plant.

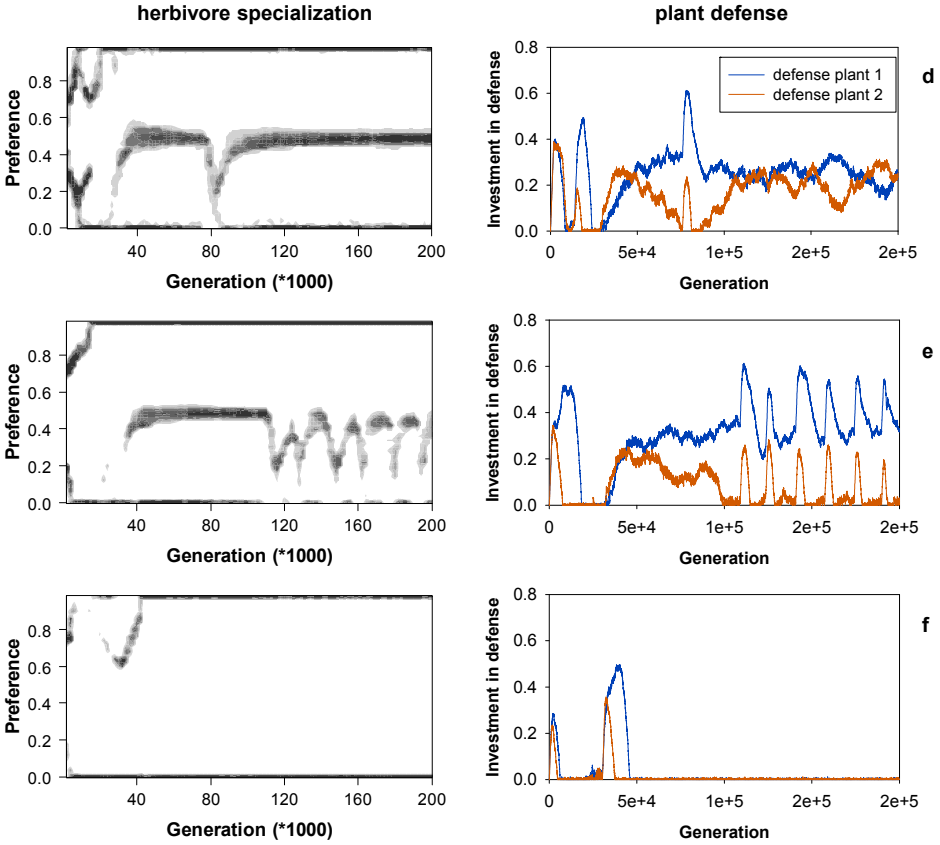

Figure 6.6 (cont.) (**d**) n = 1.5: 1 generalist + 2 specialists; both plants evolve the same intermediate level of defense. (**e**) n = 1.5: 1 specialist + branching/extinction cycles in the other herbivore; cycling in plant defense, with both plant species evolving higher defense as branching occurs and evolving lower defense as the specialist on plant 2 goes extinct. (**f**) n = 1.6: 2 specialists; both plants evolve no defense.

Supplementary material: Appendices

APPENDIX A: SUPPORTING FIGURES FOR CHAPTER 3

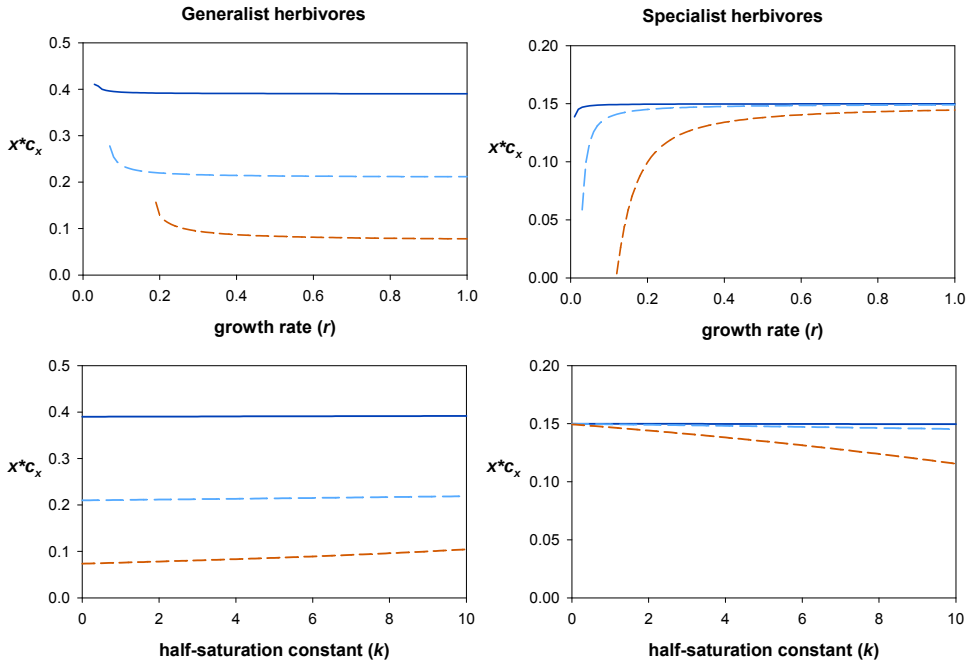

Figure A1. Numerical predictions for ESS investment depending on intrinsic growth rate (r, top panels) and the half-saturation constant for nutrient uptake (k, bottom panels) in the nutrient competition model with generalist herbivores (left) or specialist herbivores (right). Solid line: $d_P = 0.001$; long dash: $d_P = 0.01$; short dash: $d_P = 0.05$. Other parameters: $c_x = 0.1$, $e_x = 1.0$, $a = 10^{-5}$, $t_h = 0.1$, $T = 4 \cdot 10^6$. Top panels: $k = 4 \cdot 10^6$; bottom panels: $r = 0.5$. Generalist herbivores (left): $H = 10000$; specialist herbivores (right): $d_H = 0.4$, $\varepsilon = 0.25$, $c_P = 1.0$, $c_H = 2.0$.

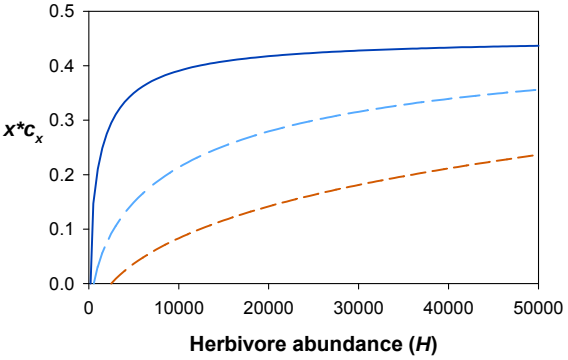

Figure A2. Numerical predictions for ESS investment depending on herbivore pressure, H, in the nutrient competition model with generalist herbivores. Solid line: d_p = 0.001; long dash: d_p = 0.01; short dash: d_p = 0.05. Other parameters: c_X = 0.1, e_X = 1.0, r = 0.5, a = 10^{-5}, t_h = 0.1, T = k = $4{\cdot}10^6$.

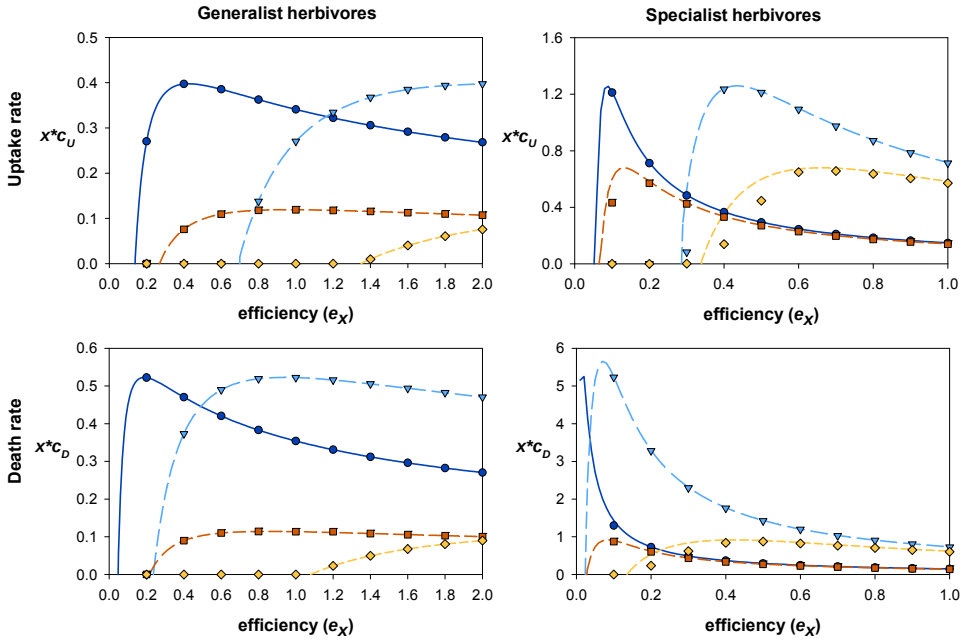

Figure A3. Numerical predictions (lines) and simulation results (symbols) for the different direct trade-offs in the nutrient competition model. Top panels: trade-off with resource uptake rate, $k(x_i) = k\left(1 + x_i c_U\right)$; bottom panels: trade-off with death rate, $d_p(x_i) = d_p\left(1 + x_i c_D\right)$. Solid line, circles: c_U, c_D = 0.1, d_p = 0.01; long dash, triangles: c_U, c_D = 0.5, d_p = 0.01; medium dash, squares: c_U, c_D = 0.1, d_p = 0.05; short dash, diamonds: c_U, c_D = 0.5, d_p = 0.05. In all panels, c_X = 0, e_X = 1.0, a = 10^{-5}, t_h = 0.1, k = T = $4{\cdot}10^6$, r = 0.5. Generalist herbivores (left): H = 10000; specialist herbivores (right): d_H = 0.4, ε = 0.25, c_P = 1.0, c_H = 2.0.

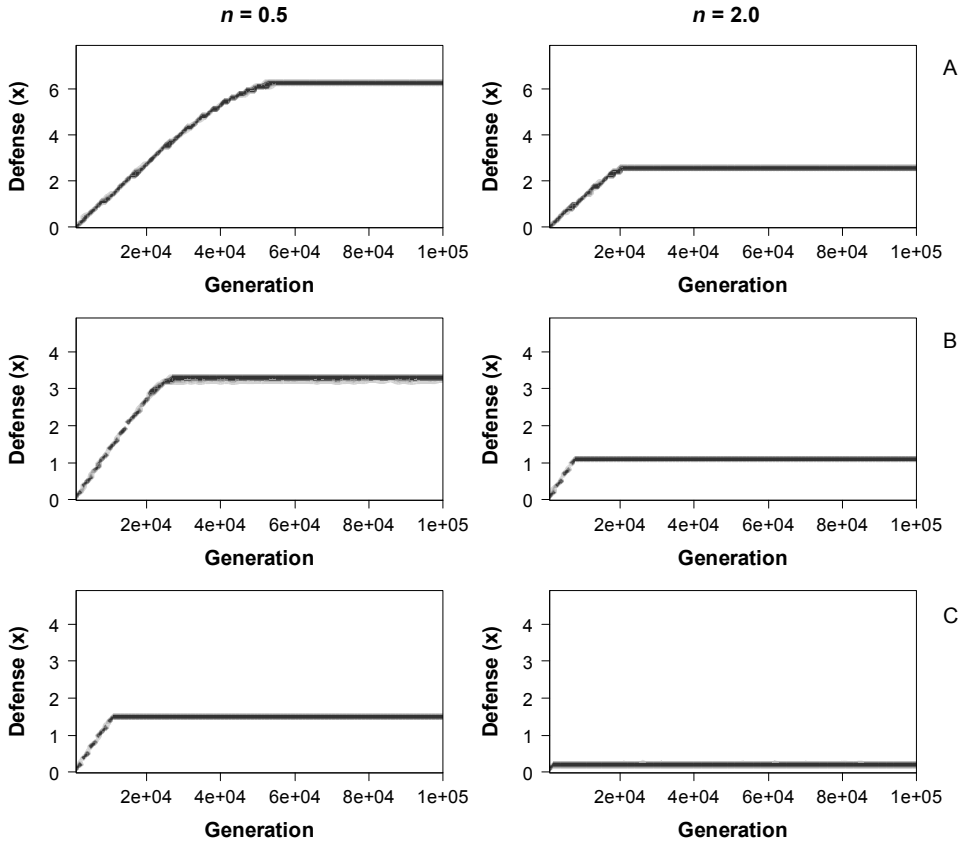

Figure A4. Examples of simulation runs for a nonlinear trade-off, $r(x(t), y(t)) = r_{max}(1-(xc_x + yc_y))^n$. Accelerating costs are present for $n < 1$, while $n > 1$ yields decelerating costs. A: Logistic growth, $K = 4{\cdot}10^6$; B: Nutrient limited growth, $T = 4{\cdot}10^6$, $d_p = 0.01$; C: Nutrient limited growth, $T = 4{\cdot}10^6$, $d_p = 0.05$. All graphs assume generalist herbivores, $H = 10000$, $r = 0.5$, $a = 10^{-5}$, $t_h = 0.1$, $c_x = 0.1$, $e_x = 1.0$.

APPENDIX B: A HERBIVORE DEFENSE MODEL WITH NON-ZERO MUTANT BIOMASS

To construct a model with a trade-off between investment and competitiveness, we need a model definition without the assumption that the mutant biomass is zero. In this version we assume Lotka-Volterra competition, where a is the intraspecific competition coefficient, and the interspecific coefficients for the resident and the mutant, α_x and $\alpha_{\hat{x}}$, depend on the trait values x and $\hat{x}$, respectively:

(B.1) $$\alpha_x = \frac{1}{1 + xc_C},\ \alpha_{\hat{x}} = \frac{1}{1 + \hat{x}c_C},$$

where c_C is the costliness of defense to competitiveness. We need to first define what the terms "intraspecific" and "interspecific" exactly refer to. For the purpose of this model, we define "intraspecific" as the effect that the specific subset of the population (e.g. clonal unit) has *on itself*, and "interspecific" as the competition with all others. So the resident's competition coefficient a_x denotes not only its competitive ability against the mutant, but also other residents. We further assume that the population is subdivided into a number of such subsets or units, which is similar to the way the simulations are set up (population subdivided into 200 lineages), so that the "mutant" has the biomass of one such unit, which we define as $p_m P(t)$.

From this we can derive the competition faced by the mutant and the residents. The mutant faces intraspecific competition from itself and interspecific competition from all the residents:

(B.2) $$C_{\hat{x}} = p_m \alpha + (1 - p_m)\alpha_x$$

The resident faces intraspecific competition from itself, and interspecific competition from both the mutant and the other residents:

(B.3) $$C_x = p_m \alpha + p_m \alpha_{\hat{x}} + (1 - 2p_m)\alpha_x$$

Because we want to keep the average competition at 1 (keeping the carrying capacity independent of the competition coefficients), both are divided by the average competition:

(B.4) $$\bar{C} = p_m C_{\hat{x}} + (1 - p_m) C_x$$

Since the competition coefficients average out, the ecological dynamics for plant biomass then look like this:

(B.5) $$\frac{dP}{dt} = P(t) r \left(1 - \frac{P(t)}{K}\right) - \left(\frac{p_m}{1 + \hat{x}(t) e_x} + \frac{(1 - p_m)}{1 + x(t) e_x}\right) \frac{HaP(t)}{1 + t_h a P(t)}$$

In the case of specialist herbivores, the herbivore dynamics change in the same way:

(B.6) $$\frac{dH}{dt} = \left(\frac{p_m}{1 + \hat{x}(t) e_x} + \frac{(1 - p_m)}{1 + x(t) e_x}\right) \frac{H(t) a P(t)}{1 + t_h a P(t)} - d_H H(t)$$

The fitness function for the mutant can be derived from the above:

(B.7) $$W = r \left(1 - \frac{C_{\hat{x}}}{\bar{C}} \frac{P^*}{K}\right) - \frac{1}{1 + x(t) e_x} \frac{Ha}{1 + t_h a P^*}.$$

Just like in a standard invasion analysis, if $W > 0$, the mutant has a higher fitness than the resident and can invade; the ESS values and stability are calculated in the same way as well. We analyzed this numerically, using a value of $p_m = 1/200$ to compare the results with the simulations that have 200 lineages. The results are shown in Figure 3.3.

APPENDIX C: A HOST-PARASITOID SIMULATION WITH FIXED POPULATION SIZES

Simulation setup: parasitoid reproduction

In this version of the model, both host and parasitoid abundances are kept constant. To determine each parasitoid's contribution to the next generation, its fitness is determined by the number of its offspring that survive larval competition, normalized over the population so the parasitoid with the most offspring has a fitness of 1. For each parasitoid of the new generation, a parent is drawn from the population with a probability equal to its fitness. The offspring parasitoid inherits the genetic traits of its parent, with some mutation as described in the Methods section of Chapter 5.

Results

The results show all the same patterns observed in the simulation with ecological host-parasitoid dynamics, confirming that the results of the original model are independent of any indirect effects of parameters on host and parasitoid abundances.

1. Single and multiple trait evolution

The results of all four single trait evolution scenarios (evolution of venom v, evolution of venom division d_V, evolution of host preference d_C with $d_V = 0.5$ and $d_V = 1.0$) closely resemble the results of the original model (compare Figure C1 with Figure 5.1), as did the results for multiple trait evolution (compare Figure C2 with Figure 5.3). For a more detailed discussion on each scenario, see the **Results** section of Chapter 5.

In addition, parasitoid population size itself has a clear effect on evolution in all three traits. A higher population size increases the superparasitism rate, leading to lower venom production (Figure C1a, C2a), a stronger bias towards injecting venom in unparasitized hosts (Figure C1b, C2b) and a stronger preference for laying eggs in unparasitized hosts (Figure C1c-d, C2c).

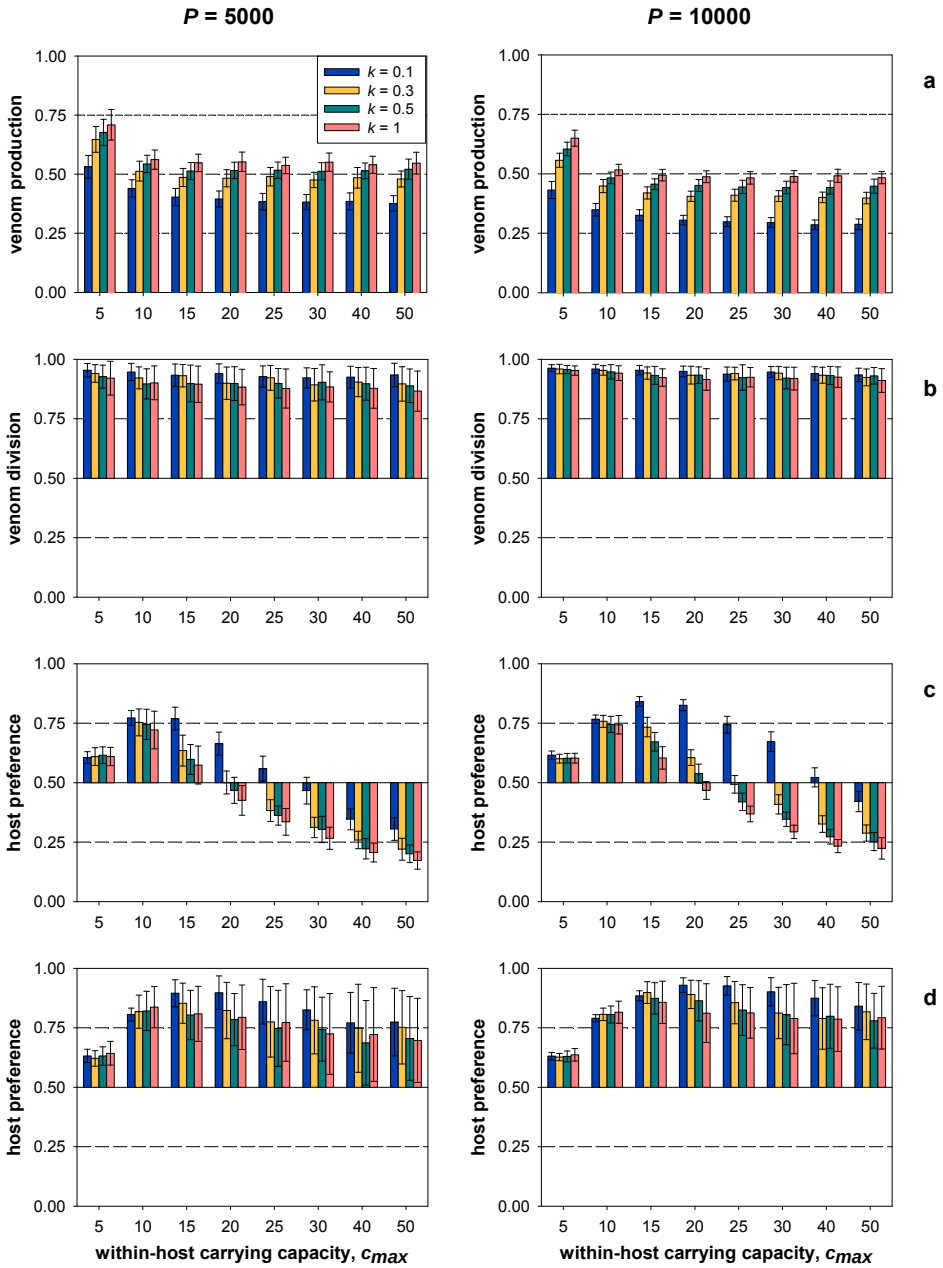

Figure C1. Single trait evolution for different values of k and c_{max}, keeping the other two traits constant. (a): evolution of venom production r; d_c = 0.5, d_v = 1.0, b = 1.0. (b): evolution of venom division d_v; v = 0.5, d_c = 0.5, b = 0. (c): evolution of host preference d_c; v = 0.5, d_v = 0.5, b = 0. (d): evolution of host preference d_c; v = 0.5, d_v = 1.0, b = 0. Other parameters: a = 3.0·10^{-5}, c_0 = 5.0, v_0 = 0.1 and H = 5000.

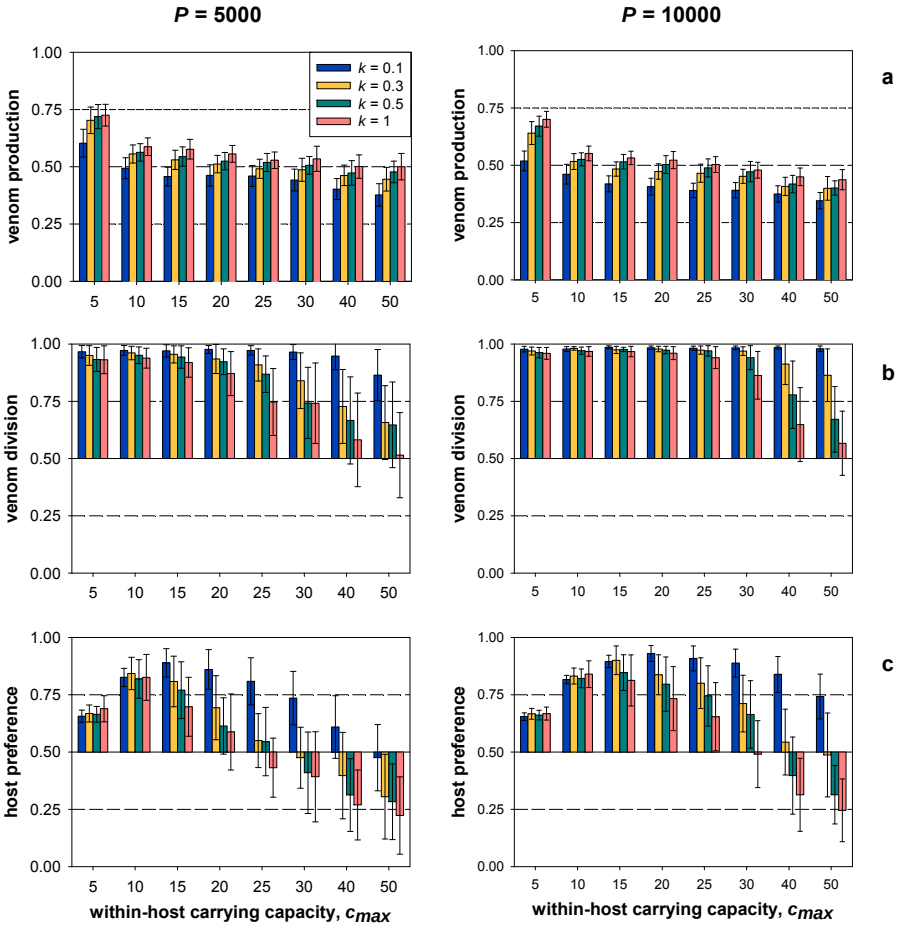

Figure C2. Simultaneous evolution of venom production, venom division and host preference. b = 1.0, v_0 = 0.1, a = 3.0·10^{-5}, c_0 = 5.0, λ = 1.3 and m = 2.0·10^{-5}.

2. Evolutionary branching and coexistence

Evolutionary branching into two parasitisation strategies was observed in this model under essentially the same conditions as the original (Figure C3). As in the original results, low within-host competition (high c_{max}), large parasitoid population sizes and a high costliness of venom production all promote both branching and coexistence. The main difference is the effect of the clumping parameter k: in contrast with the results shown in Figure 5.6, where intermediate values for k (0.3-0.7) promoted coexistence and both higher and lower values impaired it, in this model both branching and coexistence are promoted by high values for k (relatively weak clumping of encounters). Higher values for k themselves, all else remaining equal, thus promote coexistence by lowering the superparasitism rate, thereby lowering within-host competition and making superparasitism a more viable strategy. The negative effect of

high k on coexistence shown in the original results (Figure 5.6) can be explained by the fact that parasitoid population size decreases with k, thereby reducing the probability that coexistence is stable in the long run.

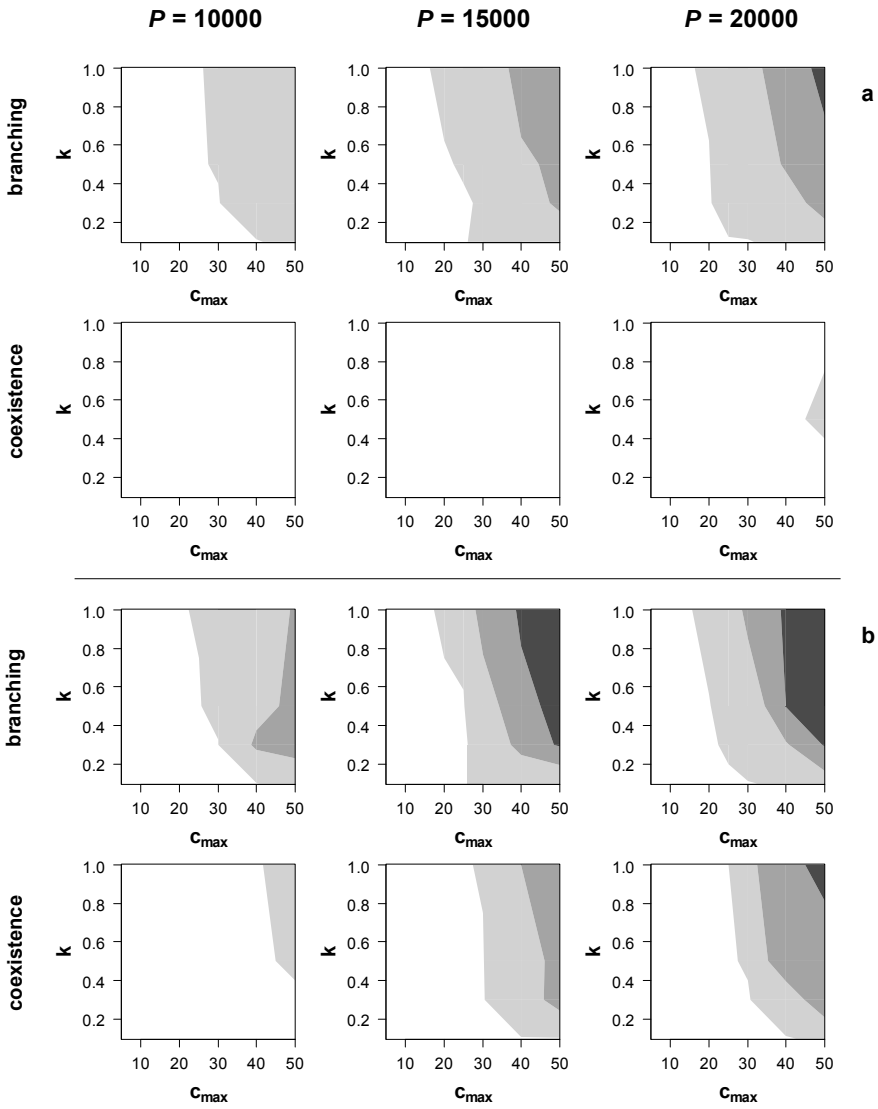

Figure C3. The frequency of evolutionary branching and coexistence of two strategies, for three values for parasitoid abundance P. (a): low cost, $b = 1.0$; (b): high cost, $b = 2.0$. Other parameters: $H = 5000$, $a = 3.0 \cdot 10^{-5}$, $c_0 = 5.0$, $v_0 = 0.1$. Colours denote the frequency, scored over 50 replicate simulation runs. White: no branching / coexistence; light grey: 0-50%; middle grey: 50-95%; dark grey: >95%.

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Summary

Samenvatting

SUMMARY

Ecology and evolutionary biology have traditionally been regarded as separate fields; this separation has, to a large extent, been driven by the common long-held belief that ecological and evolutionary dynamics operate on such different timescales that they do not affect each other. However, as both ecological (population) dynamics and individual fitness are ultimately determined by the number of offspring produced by each individual in the population, ecological and evolutionary dynamics are obviously closely intertwined. As evidence for rapid evolution in nature has accumulated, recent years have seen a renewed interest in the interplay between ecology and evolution (eco-evolutionary dynamics or eco-evolutionary feedbacks). With it has come a growing appreciation that the close entanglement of ecology and evolution means that studying either process in isolation gives a very limited view on for example population dynamics, consumer-resource interactions and coexistence. A growing body of theoretical models has shown that the combined effect of ecological and evolutionary dynamics can be very different from what would be predicted considering either one by itself.

Research on eco-evolutionary dynamics has largely focused on trophic interactions, mainly in predator-prey systems. There are two reasons for this: first, the traits that determine interspecies interactions (e.g. predator attack rate on different prey, or level of prey defense against predation), and thereby the ecological dynamics of the system, are the same traits that determine individual fitness, thereby making them prime candidates for eco-evolutionary feedbacks. Second, because the strong selection pressures exerted by predator-prey interactions can drive rapid evolutionary change, thereby making eco-evolutionary feedbacks more likely.

In this thesis, I studied eco-evolutionary dynamics in the context of trophic interactions in two types of systems: plant-herbivore interactions and multiparasitoid-host interactions. My main focus was to study the effect of eco-evolutionary dynamics on the evolution and coexistence of divergent strategies in the trophic level under study (herbivores, **chapter 2**; plants, **chapter 3**; and parasitoids, **chapters 4** and **5**).

Evolution and coexistence in a plant-herbivore system (chapters 2 and 3)

In **chapter 2** I studied the evolutionary origins and coexistence of generalist and specialist herbivores (or, more generally, consumers) on two plant (resource) species. For this purpose I modified a well-established model for generalist-specialist coexistence to allow for competition on the lower level (resources, in this case plants) to study its effects on herbivore evolution. In this model, specialists have a selective advantage over generalists when plant abundances are relatively constant, being more efficient in consuming their preferred plant species than a generalist is in consuming either; but strong fluctuations in plant abundances give an advantage to generalists being able to consume both.

Competition between plants, though seemingly a minor addition to the model, caused an extra ecological feedback to be added to the system, generating very different evolutionary

dynamics from a system without competition. The difference in which combination of herbivore specialization strategies could evolve and coexist was dramatic: the number of different combinations increased from the three found in models without competition to seven.

The four new outcomes included three different kinds of evolutionary cycling driven by eco-evolutionary feedbacks: as new herbivore strategies evolved, the ecological dynamics changed, in turn changing the fitness landscapes for the herbivores. Sometimes this meant that previously viable strategies suddenly became unviable and were driven extinct. For example, coexistence of just two specialist herbivores gives rise to strong fluctuations in plant abundance, a condition that gives a selective advantage to generalists; however, as a generalist evolved the fluctuations were dampened by its presence, decreasing its advantage and, under some conditions (a strong trade-off conferring an advantage to specialists) driving the generalist extinct, after which the cycle repeated. This type of evolutionary cycling is not seen in models without between-plant competition; it is driven by the eco-evolutionary feedback caused by competition on the plant level.

In **chapter 3** I studied the evolution of defense against herbivory in plants in a herbivore-plant model, assuming consumption by a single herbivore (either generalist or specialist). A higher level of defense reduces biomass loss through herbivory, but comes at a cost: either a reduced growth rate (*direct* cost) or reduced intraspecific competitiveness (*ecological* cost, expressed only through ecological interactions, in this case intraspecific competition). Several patterns emerged, indicating a large effect both of the type of trade-off (direct vs. ecological) and the type of herbivore (generalist vs. specialist). Most strikingly, evolutionary branching into defending and non-defending plants, and stable coexistence of these two strategies, was only possible when the trade-off affected competitiveness.

The effect of eco-evolutionary feedbacks was demonstrated by the difference between models with generalist and specialist herbivores: I assume that specialist herbivores are dependent on the focal plant species, and decrease in numbers when it becomes unavailable (through either low abundance or high defense), while this is not the case for generalist herbivores which can feed on other plant species. This led to several differences in model predictions. First, against generalist herbivores, a higher efficiency of defense always led to a higher investment in defense; against specialist herbivores the effect of efficiency was non-monotonic, with the highest investment occurring for intermediate efficiency. Second, increasing nutrient availability had opposing effects on defense against generalists and specialists: against generalists, a higher nutrient availability led to lower defense, while the converse was true for defense against specialists. And finally, while an ecological trade-off caused evolutionary branching into two defense strategies against both generalists and specialists, long-term coexistence was only possible when the herbivores were generalists. After branching had taken place, specialist herbivores would increase in numbers driven by the newly available low-defense plants, driving them extinct. The presence of only high-defense plants would subsequently drive down herbivore abundance, in turn allowing the remaining plants to lower their level of defense, after which evolutionary branching would occur again.

The results of these two chapters indicate that feedbacks between ecological and evolutionary dynamics can destabilize coexistence. In both models, evolutionary cycling including branching-extinction cycles are observed when eco-evolutionary feedbacks are present.

Coexistence in a multiparasitoid-host system (chapters 4 and 5)

In **chapters 4** and **5**, I modelled a multiparasitoid-host system inspired by coexistence of two *Nasonia* species in Eastern North America: *N. vitripennis* and *N. giraulti*. Though *N. giraulti* is an inferior competitor, having a lower fecundity and longer development time than *N. vitripennis*, the two species can coexist despite strong distribution overlap and a high multiparasitism rate in the field (females of both species parasitizing the same hosts). Because *N. giraulti* has been shown to prefer multiparasitizing (parasitizing a host already parasitized by *N. vitripennis*) over parasitizing a fresh host, I hypothesized that within-host competition may play a role in the coexistence of these two species. I constructed two models: a purely ecological model (**chapter 4**) and a model including evolution (**chapter 5**), with a focus on the conditions that would allow coexistence of the two parasitoid species, which turned out to be very different between the two models.

In **chapter 4**, I focused on two factors that may explain why a parasitoid with a lower fecundity (*N. giraulti*) may coexist with a superior competitior (*N. vitripennis*): first, weak within-host competition (a high within-host carrying capacity, allowing the offspring of multiple females to share the host without strong negative effects on offspring survival); and second, a within-host competitive advantage for the lower-fecundity species. Somewhat surprisingly I found that the first factor, weak within-host competition, strongly impaired coexistence. The second, asymmetric within-host competition, can promote coexistence, but again under the condition that within-host competition is severe; in addition, the overlap in host use must be neither too small (because a within-host advantage will have little effect) nor too large (because the superior competitor within the host will outcompete the other species). Because the overlap in the distributions of *N. vitripennis* and *N. giraulti* in the field is very high, I conclude that neither factor is likely to explain the coexistence of these two species.

Next I considered an evolutionary model for the same system (**chapter 5**). I here studied an evolutionary individual-based simulation in which the parasitoids' parasitization strategy could evolve (whether they have a preference for laying eggs in unparasitized vs. already parasitized hosts). The latter has the disadvantage of increasing the level of within-host competition, lowering offspring survival. On the other hand, it may allow the superparasitizing female to economize on the production of venom needed to kill the host; or alternatively, the double dose of venom may increase the probability of successfully killing the host. I simulated the simultaneous evolution of venom production and host preference and found, in part of the parameter range, evolutionary divergence into two distinct parasitization strategies: producing venom and preferring unparasitized hosts; and producing no venom and preferring parasitized hosts, taking advantage of the venom injected by the first female. The two strategies can stably coexist, but only when the within-host carrying capacity is high (weak within-host

competition); notably, this is exactly the same condition that impaired coexistence in the purely ecological model.

The results of these two models lead to the conclusion that in this case, eco-evolutionary dynamics can lead to stable coexistence under conditions where ecological dynamics alone would preclude it.

Future directions

In **chapter 6**, I show some preliminary results that indicate what I believe to be interesting directions for future research.

The effect of the speed of evolutionary dynamics relative to ecological dynamics is currently a subject of intense debate, with rapid evolution being particularly implicated in eco-evolutionary feedbacks; however, the effect of the speed of evolution on stability and coexistence in models such as I have presented here is far from clear. Preliminary results on varying the mutation rate in herbivore evolution (see **chapter 2**) suggest that rapid evolution is more likely to lead to evolutionary cycling and branching-extinction cycles; slow evolution, on the other hand, is more likely to lead to stable coexistence. However, the range of mutation rates studied is still relatively narrow; these results cannot be safely extrapolated to very slow or very fast evolution. Moreover, what the effect of varying the mutation rate would be in any of the other ecological scenarios in this thesis is an open question.

While models on the evolution and coexistence of generalists and specialists traditionally use two resources (as I assumed two plant species in **chapter 2**), evolution in nature usually occurs in far more complex communities. I took one step in this direction by extending the two-plant model to three plant species, and observing the effect of this change on the combinations of generalist and specialist herbivores that evolved. Probably the most striking result of this modification is that no evolutionary cycling was observed in any of the simulation runs, while evolutionary cycling was common in the two-plant model. A second main result is that the number of herbivore strategies coexisting never exceeded the number of plant species, while this is commonly observed in two-resource models (three consumers, two specialists and a generalist, coexisting on two resources, as long as resource abundances fluctuate). These results are very preliminary, and what causes these major divergences from predictions by two-resource models is far from clear. However, it suggests that studying evolution in more complex communities may be one of the most important avenues for future research, as results from simple communities may be easier to understand, but cannot be extrapolated to more complex ones.

Lastly, I studied the effect of co-evolution between plants (evolving defense against herbivory, **chapter 3**) and herbivores (evolving degree of specialization, **chapter 2**). While the interaction between plant and herbivore evolution leads to complex results, and interpreting them in detail is beyond the scope of the thesis, some general patterns emerge. First, stable coexistence of herbivore strategies is more common in the co-evolution model, with a marked decrease in all types of evolutionary cycling. Second, including the evolution of plant defense invariably leads to a higher degree of specialization in the herbivores. Conversely, a lower level

of defense evolves against specialist herbivores than against generalists, usually leading to both plants evolving a no-defense strategy when herbivores are completely specialized. This leads to the seemingly paradoxical result that complete herbivore specialization occurs for a much broader parameter range than in the model without plant evolution, but this is not commonly associated with any degree of defense in the plants. The effects of interaction between plant defense and herbivore specialization are not always straightforward either: with both plants and herbivores evolving in response to one another, the combinations of plant and herbivore strategies that can result are many and varied, and sometimes contradictory; making sense of it will be an important challenge for future research.

In conclusion

The importance of the interplay between ecological and evolutionary dynamics has seen increasing appreciation in recent years, but straightforward answers on how this affects evolution and coexistence in competitors are still forthcoming. Under which scenarios, for which types of interactions or traits, are eco-evolutionary dynamics likely to stabilize or destabilize a system? What does this mean for predictions on population persistence, particularly in the context of environmental change? The difficulty in finding answers to these open questions is reflected in the results of this thesis: in some scenarios, eco-evolutionary dynamics lead to extinctions or evolutionary suicide; in others it can promote stable coexistence. Moreover, even under conditions where evolution stabilizes ecological dynamics, this does not necessarily lead to more stable eco-evolutionary dynamics.

The aim of this thesis was to study specific ecological scenarios rather than answer the overarching general questions; but the contradictory nature of the results and conclusions are an indication that a proper, systematic study of the general questions is really necessary. This will probably be the main challenge in the field of eco-evolutionary dynamics in the near future.

SAMENVATTING

Ecologie en evolutiebiologie zijn van oudsher als twee gescheiden velden van studie beschouwd; een belangrijke reden voor deze scheiding was het feit dat lang werd gedacht dat ecologische en evolutionaire processen op tijdschalen plaatsvinden die zo verschillend zijn dat ze elkaar niet kunnen beïnvloeden. Aan de andere kant worden zowel ecologische (populatie-) dynamica en individuele fitness uiteindelijk bepaald door het aantal nakomelingen van ieder individu in de populatie, waardoor ecologische en evolutionaire dynamica overduidelijk onlosmakelijk met elkaar zijn verbonden. In recente jaren is steeds meer bewijs voor snelle evolutie in natuurlijke systemen verzameld, wat voor een hernieuwde interesse in de samenwerking tussen ecologie en evolutie (eco-evolutionaire dynamica of eco-evolutionaire feedbacks) heeft gezorgd. Hierdoor is het steeds duidelijker geworden dat, door de nauwe verwikkeling van ecologie en evolutie, het bestuderen van één van de twee onafhankelijk van de andere een beperkt inzicht geeft in bijvoorbeeld populatiedynamica, interacties tussen organismen en hun voedsel, of coëxistentie. Steeds meer theoretische modellen laten zien dat het gecombineerde effect van ecologie en evolutie heel verschillend kan zijn dan wat je zou verwachten afgaande op modellen die maar één van de twee bestuderen.

Een groot deel van onderzoek naar eco-evolutionaire dynamica is gericht op trofische interacties, voornamelijk predator-prooi systemen. Hier zijn twee redenen voor: ten eerste, de eigenschappen die interacties tussen soorten bepalen (bijvoorbeeld de mate waarin een predator verschillende prooien aanvalt, of de mate waarin de prooi zich verdedigt tegen predatoren), en daardoor de ecologische dynamica van het systeem beïnvloeden, zijn dezelfde eigenschappen die de fitness van individuen bepalen, waardoor ze waarschijnlijk een grote rol spelen in eco-evolutionaire feedbacks. Ten tweede is de selectiedruk in predator-prooi systemen vaak zo sterk dat ze snelle evolutionaire verandering kunnen veroorzaken, waardoor eco-evolutionaire feedbacks waarschijnlijker zijn.

In dit proefschrift bestudeerde ik eco-evolutionaire dynamica in de context van trofische interacties in twee systemen: interacties tussen planten en herbivoren, en tussen meerdere parasitoïden en hun gastheren. Mijn doel was het bestuderen van de invloed van eco-evolutionaire dynamica op de evolutie en coëxistentie van verschillende strategieën in het trofische niveau onder studie (herbivoren, **hoofdstuk 2**; planten, **hoofdstuk 3**; en parasitoïden, **hoofdstuk 4 en 5**).

Evolutie en coëxistentie in een planten-herbivoren system (hoofdstukken 2 en 3)

In **hoofdstuk 2** bestudeerde ik de evolutionaire oorsprong van en coëxistentie tussen generalistische en gespecialiseerde herbivoren (of meer algemeen "consumenten") op twee plantensoorten (bronnen). Hiervoor paste ik een bestaand model voor coëxistentie tussen generalisten en specialisten aan, door competitie tussen de soorten op het lagere niveau (in dit

geval planten) mogelijk te maken, om het effect daarvan op de evolutie van herbivoren te bestuderen. In dit model hebben specialisten een selectief voordeel ten opzichte van generalisten wanneer de abundantie van planten relatief constant is, omdat ze efficiënter zijn in het consumeren van hun geprefereerde plantensoort dan de generalist; maar sterke fluctuaties in de abundanties van planten geven een voordeel aan generalisten, omdat ze beide plantensoorten kunnen consumeren.

Hoewel de toevoeging van competitie tussen planten een kleine modificatie van het model lijkt, leidde het tot een extra ecologische feedback in het systeem, waardoor heel andere evolutionaire dynamica werden gegenereerd dan in een systeem zonder competitie. Het leidde tot een dramatisch verschil in welke combinaties van specialisatie-strategieën konden evolueren en naast elkaar bestaan: het aantal verschillende combinaties liep op van de drie die in modellen zonder competitie kunnen worden gevonden tot zeven.

Onder de vier nieuwe uitkomsten waren drie verschillende vormen van evolutionaire cycli, gedreven door eco-evolutionaire feedbacks: de evolutie van nieuwe strategieën onder de herbivoren veranderde de ecologische dynamica, die op hun beurt de fitnesslandschappen voor de herbivoren veranderden. Soms betekende dit dat bestaande strategieën plotseling niet langer levensvatbaar waren, en tot uitsterven werden gedreven. Wanneer twee specialisten naast elkaar bestaan, bijvoorbeeld, zorgt dit voor sterke fluctuaties in de abundanties van planten, waardoor generalisten een voordeel hebben en kunnen evolueren; maar wanneer een generalist evolueert, dempte zijn eigen aanwezigheid de fluctuaties, waardoor zijn voordeel vermindert of zelfs helemaal verdwijnt. Onder sommige omstandigheden (een sterke trade-off die een groot voordeel geeft aan specialisten) stierf de generalist uit, waarna de cyclus zich herhaalde. Dit soort evolutionaire cycli vinden niet plaats in modellen zonder competitie; ze worden gegenereerd door de eco-evolutionaire feedback die wordt veroorzaakt door competitie tussen de planten.

In **hoofdstuk 3** bestudeerde ik de evolutie van verdediging tegen herbivorie in planten in een herbivoor-plant model, aannemend dat de plant door een enkele herbivoor wordt geconsumeerd (een generalist of een specialist). Een hogere mate van verdediging vermindert het verlies van biomassa door herbivorie, maar heeft ook een nadeel: een lagere maximale groeisnelheid (een *direct* nadeel) of een verminderde intraspecifieke competitieve kwaliteit (een *ecologisch* nadeel, dat alleen tot uiting komt door ecologische interacties, in dit geval intraspecifieke competitie). Verscheidene patronen kwamen naar voren, duidend op een sterk effect van zowel het type trade-off (direct of ecologisch) en het type herbivoren (generalisten of specialisten). Het meest opvallende resultaat was dat evolutionaire vertakking in verdedigende en niet-verdedigende planten, en stabiele coëxistentie van deze twee strategieën, alleen mogelijk was onder een ecologische trade-off.

Het effect van eco-evolutionaire feedbacks werd gedemonstreerd door het verschil tussen modellen met generalisten en specialisten als herbivoren: mijn aanname was dat gespecialiseerde herbivoren afhankelijk zijn van de plantensoort onder studie, en dat hun aantallen afnemen wanneer die soort niet beschikbaar is (door lage abundantie of sterke verdediging tegen herbivorie), maar dat dit niet het geval is voor generalisten die ook andere plantensoorten tot hun beschikking hebben. Dit zorgde voor een aantal verschillen in

modelvoorspellingen. Ten eerste, tegen een generalist zorgde meer efficiënte verdediging altijd voor een hogere investering in verdediging; tegen een specialist was het effect van efficiëntie niet-monotoon, en de hoogste investering in verdediging werd gevonden voor middelmatige efficiëntie. Ten tweede had een toename van nutriënten in het systeem tegengestelde effecten op verdediging tegen generalisten en specialisten: tegen generalisten zorgden meer nutriënten voor een lagere verdediging, maar tegen specialisten was het omgekeerde waar. En tenslotte was evolutionaire vertakking in twee verdedigingsstrategieën te zien tegen zowel specialisten als generalisten, maar stabiele coëxistentie was alleen mogelijk in verdediging tegen generalisten. Dit is omdat na vertakking specialisten in aantallen toenamen door de beschikbaarheid van laag-verdedigende planten, waardoor ze deze planten tot uitsterven dreven. De aanwezigheid van alleen hoog-verdedigende planten dreef daarna de abundantie van herbivoren weer naar beneden, waardoor de planten op hun beurt tot lagere verdediging konden evolueren, waarna evolutionaire vertakking opnieuw plaatsvond.

De resultaten van deze twee hoofdstukken laten zien dat feedbacks tussen ecologische en evolutionaire dynamica coëxistentie kunnen destabiliseren. In beide modellen zorgen eco-evolutionaire feedbacks voor cycli van vertakking en extinctie, waar deze niet plaatsvinden in modellen zonder deze feedbacks.

Coëxistentie in een multiparasitoïd-gastheer systeem (hoofdstukken 4 en 5)

In **hoofdstukken 4** en **5** modelleerde ik een multiparasitoïd-gastheer systeem, geïnspireerd door de coëxistentie van twee *Nasonia*-soorten in Noord-Oost-Amerika: *N. vitripennis* en *N. giraulti*. Hoewel *N. giraulti* een inferieure concurrent is, met een lagere fecunditeit en een langere ontwikkelingstijd dan *N. vitripennis*, kunnen deze twee soorten naast elkaar bestaan, ondanks hun grote overlap in distributie en een hoge frequentie van multiparasitisme (dezelfde gastheer wordt door vrouwtjes van beide soorten geparasiteerd) in de natuur. Omdat *N. giraulti* een voorkeur lijkt te hebben voor multiparasitisme (parasiteren van een gastheer die al is geparasiteerd door *N. vitripennis*), zelfs als de keuze is tussen multiparasitisme en het parasiteren van een lege gastheer, speculeerde ik dat competitie binnen de gastheer een rol zou kunnen spelen bij de coëxistentie van deze twee soorten. Ik maakte twee modellen: een model met alleen ecologische dynamica (**hoofdstuk 4**) en een model waarin ook evolutie mogelijk was (**hoofdstuk 5**), met het doel de voorwaarden voor coëxistentie te vinden. Deze bleken sterk te verschillen tussen deze twee modellen.

In **hoofdstuk 4** richtte ik me op twee factoren die zouden kunnen verklaren hoe een parasitoïd met een lagere fecunditeit (*N. giraulti*) kan voortbestaan naast een superieure concurrent (*N. vitripennis*): ten eerste, lage competitie binnen de gastheer (een hoge draagkracht binnen de gastheer, waardoor de nakomelingen van meerdere vrouwtjes de gastheer kunnen delen zonder sterke negatieve gevolgen voor hun overlevingskansen); en ten tweede, een voordeel in competitie binnen de gastheer voor de soort met lagere fecunditeit. Tot mijn verrassing ontdekte ik dat de eerste factor, lage competitie binnen de gastheer, een sterk negatief effect had op coëxistentie. De tweede factor, asymmetrische competitie binnen de gastheer, kan coëxistentie bevorderen, maar opnieuw alleen als competitie binnen de gastheer

hoog is. Bovendien moest de overlap in gebruik van de gastheren tussen de soorten niet te klein zijn (omdat een voordeel binnen de gastheer dan weinig effect heeft), en niet te groot (omdat de soort met het voordeel binnen de gastheer de andere soort dan kan verdringen). Omdat de overlap tussen *N. vitripennis* en *N. giraulti* in de natuur heel groot is, concludeer ik dat geen van beide factoren een waarschijnlijke verklaring is voor coëxistentie van deze twee soorten.

Vervolgens beschouwde ik een evolutionair model voor hetzelfde systeem (**hoofdstuk 5**). Hier bestudeerde ik een simulatie gebaseerd op individuen, waarin de parasitisme-strategie van de parasitoïden kon evolueren (of ze een voorkeur hadden voor het leggen van eitjes in niet-geparasitseerde of al geparasiteerde gastheren). De tweede strategie heeft als nadeel dat competitie binnen de gastheer hoger is, wat nadelig is voor de overleving van nakomelingen. Aan de andere kant kan een superparasiterend vrouwtje zich de kosten besparen van het produceren van gif om de gastheer te doden; of superparasitisme leidt tot een dubbele dosis gif, waardoor de kans dat de gastheer gedood wordt groter is. Ik simuleerde de gelijktijdige evolutie van gifproductie en gastheer-voorkeur en vond, voor een deel van de parameterwaarden, evolutionaire splitsing in twee heel verschillende parasitisme-strategieën: een voorkeur voor niet-geparasiteerde gastheren, gekoppeld met gifproductie; en een voorkeur voor geparasiteerde gastheren, waarbij de parasitoïden met deze strategie zelf geen gif produceren, maar gebruik maken van het gif dat door het eerste vrouwtje is geïnjecteerd. Deze twee strategieën kunnen op de lange termijn naast elkaar bestaan, maar alleen wanneer de draagkracht van de gastheren hoog is (lage competitie tussen nakomelingen binnen de gastheer). Opvallend is dat dit precies dezelfde voorwaarde is die coëxistentie onmogelijk maakte in het model met alleen ecologische dynamica.

De resultaten van deze twee modellen leiden tot de conclusie dat in dit geval, eco-evolutionaire dynamica tot stabiele coëxistentie kunnen leiden, waar dit niet mogelijk is wanneer alleen ecologische dynamica in beschouwing worden genomen.

Ideeën voor vervolgonderzoek

In **hoofdstuk 6** laat ik wat voorlopige resultaten zien die wijzen op wat ik beschouw als veelbelovende richtingen voor vervolgonderzoek.

Het effect van de relatieve snelheden van evolutionaire en ecologische veranderingen is momenteel het onderwerp van intensief debat, waarbij vooral wordt gedacht dat snelle evolutie een belangrijke rol speelt in eco-evolutionaire feedbacks; maar het effect van de snelheid van evolutie op stabiliteit en coëxistentie in de modellen die ik hier heb gepresenteerd is verre van duidelijk. De eerste resultaten van het variëren van de mutatiesnelheid in de evolutie van herbivoren (zie **hoofdstuk 2**) duiden erop dat snelle evolutie vaker tot evolutionaire cycli en vertakking-extinctie cycli leidt; langzame evolutie, aan de andere kant, leidt vaker tot stabiele coëxistentie. Echter, de variatie in mutatiesnelheden die hier bestudeerd is, is nog altijd vrij klein; deze resultaten kunnen niet simpel geëxtrapoleerd worden naar extreem langzame of extreem snelle evolutie. Bovendien is het effect van de mutatiesnelheid op de andere ecologische scenario's in dit proefschrift nog altijd een open vraag.

Hoewel modellen voor de evolutie en coëxistentie van generalisten en specialisten altijd twee bronnen gebruiken (zie mijn aanname van twee plantensoorten in **hoofdstuk 2**), vindt evolutie in de natuur plaats in veel complexere gemeenschappen. Ik heb één stap in deze richting gezet door het twee-planten-model uit te breiden naar drie plantensoorten, en te kijken naar hoe deze verandering invloed had op de combinaties van generalisten en specialisten die evolueerden. Waarschijnlijk het meest opvallende resultaat van deze modificatie is dat in geen enkele van de simulaties evolutionaire cycli werden waargenomen, waar dit wel vaak gebeurde in het twee-planten-model. Het tweede belangrijke resultaat was dat het aantal herbivoren-strategieën dat naast elkaar kon bestaan nooit het aantal plantensoorten overschreed, een resultaat dat wel vaak gezien wordt in modellen met twee bronnen (drie consumenten, twee specialisten en één generalist, kunnen naast elkaar bestaan op twee bronnen, als er fluctuaties zijn in de beschikbaarheid van de bronnen). Deze resultaten zijn nog in een vroeg stadium, en wat deze sterke afwijkingen ten opzichte van voorspellingen van het twee-planten-model veroorzaakt is verre van duidelijk. Maar het is een duidelijke aanwijzing dat evolutie in meer complexe gemeenschappen mogelijk één van de belangrijkste richtingen voor toekomstig onderzoek is, omdat resultaten van te vereenvoudigde gemeenschappen misschien makkelijker te doorgronden zijn, maar niet kunnen worden geëxtrapoleerd naar complexere systemen.

Als laatste bestudeerde ik het effect van co-evolutie tussen planten (evolutie van verdediging tegen herbivorie, **hoofdstuk 3**) en herbivoren (evolutie van mate van specialisatie, **hoofdstuk 2**). Hoewel de interactie tussen evolutie in planten en herbivoren tot complexe resultaten leidt, en de interpretatie daarvan buiten het bereik van dit proefschrift ligt, worden verschillende patronen duidelijk. Ten eerste is stabiele coëxistentie van verschillende herbivorie-strategieën meer waarschijnlijk in het co-evolutie model, met een duidelijke afname in alle vormen van evolutionaire cycli. Ten tweede leidt de evolutie van verdediging in planten altijd tot meer specialisatie in de herbivoren. Tegelijkertijd evolueren planten altijd een lagere mate van verdediging tegen specialisten dan tegen generalisten, met de gebruikelijke uitkomst dat beide plantensoorten een niet-verdedigende strategie evolueren tegen twee volledig gespecialiseerde herbivoren. Dit leidt tot het ogenschijnlijk paradoxale resultaat dat complete specialisatie over een groter parameterbereik plaatsvindt dan in het model zonder evolutie in planten, maar deze uitkomst is gewoonlijk niet geassocieerd met enige mate van verdediging in planten. Het effect van interactie tussen de evolutie van verdediging in planten en van specialisatie in herbivoren is ook niet altijd eenduidig: omdat de evolutie in planten en herbivoren op elkaar reageren, zijn veel verschillende combinaties van strategieën in planten en herbivoren mogelijk die soms in tegenspraak met elkaar zijn; het vinden van duidelijkheid in deze scenario's is waarschijnlijk één van de grootste uitdagingen voor toekomstig onderzoek.

Conclusie

In de laatste jaren is het belang van de interactie tussen ecologische en evolutionaire dynamics steeds duidelijker geworden, maar eenduidige antwoorden over de invloed hierop op de evolutie en coëxistentie van concurrenten zijn er nog altijd niet. Onder welke scenario's, voor welke types interacties tussen of eigenschappen van soorten, is het waarschijnlijk dat het

systeem door eco-evolutionaire dynamica wordt gestabiliseerd of gedestabiliseerd? Wat betekent dit voor de levensduur van populaties, in het bijzonder in de context van klimaatverandering? Hoe moeilijk het is om antwoorden op deze open vragen te vinden wordt opnieuw duidelijk in de resultaten in dit proefschrift: in sommige scenario's leiden eco-evolutionaire dynamica tot uitstervingen of evolutionaire zelfmoord; in andere kunnen ze stabiele coeëxistentie bevorderen. En zelfs wanneer evolutie de ecologische dynamica stabiliseert, leidt dit niet noodzakelijkerwijs tot stabielere eco-evolutionaire dynamica.

Het doel van dit proefschrift was om specifieke ecologische scenario's te bestuderen, en niet zozeer om de overkoepelende algemene vragen te beantwoorden, maar de tegenstrijdige resultaten en conclusies in dit proefschrift zijn een teken dat systematisch onderzoek naar de algemene vragen absoluut noodzakelijk is. Dit is waarschijnlijk voor de nabije toekomst de grootste uitdaging in het veld van eco-evolutionaire dynamica.

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